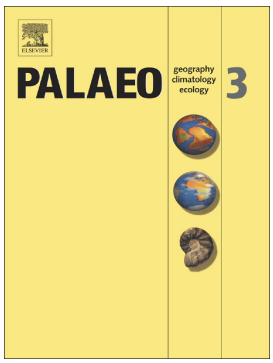
Accepted Manuscript



Arab-Madagascan brachiopod dispersal along the North-Gondwana paleomargin towards the Western Tethys Ocean during the Early Toarcian (Jurassic)

José Francisco Baeza-Carratalá, Fernando García Joral, Antonio Goy, José Enrique Tent-Manclús

PII: S0031-0182(17)30739-3
DOI: doi:10.1016/j.palaeo.2017.11.004
Reference: PALAEO 8505

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 10 July 2017
Revised date: 2 October 2017
Accepted date: 1 November 2017

Please cite this article as: José Francisco Baeza-Carratalá, Fernando García Joral, Antonio Goy, José Enrique Tent-Manclús , Arab-Madagascan brachiopod dispersal along the North-Gondwana paleomargin towards the Western Tethys Ocean during the Early Toarcian (Jurassic). The address for the corresponding author was captured as affiliation for all authors. Please check if appropriate. Palaeo(2017), doi:10.1016/j.palaeo.2017.11.004

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

ACCEPTED MANUSCRIPT

Arab-Madagascan brachiopod dispersal along the North-Gondwana paleomargin towards the Western Tethys Ocean during the Early Toarcian (Jurassic)

José Francisco Baeza-Carratalá[1*], Fernando García Joral[2], Antonio Goy[2], José Enrique Tent-Manclús[1]

[1]Departamento de Ciencias de la Tierra y Medio Ambiente, Universidad Alicante, Apdo. 99, San Vicente del Raspeig, 03080 Alicante, Spain.

[2]Departamento de Paleontología, Facultad de Ciencias Geológicas. Universidad Complutense. C/ José Antonio Novais, 2; 28040, Madrid. Spain.

*Corresponding author. E-mail addresses: jf.baeza@ua.es (JFBC); fgjoral@geo.ucm.es (FGJ); angoy@geo.ucm.es (AG); je.tent@ua.es (JETM).

Abstract

Multiple approaches, mainly focused on assessing the depositional environments, paleotemperature, chronostratigraphical and paleobiogeographical data, morphometrical analyses and the study of the internal structure of spiriferinide brachiopods assigned to the genus *Calyptoria*, have revealed that this brachiopod fauna migrated from their Arab-Madagascan homeland along the North-Gondwana paleomargin into the peri-Iberian epicontinental platform system, in the same well-known spreading episode suffered by the Arab-Madagascan *Bouleiceras* ammonite fauna over the worldwide-distributed early Toarcian platforms. This brachiopod fauna has been so far overlooked as potential Arab-Madagascan immigrant fauna, as it was integrated together with diverse assemblages well-established in the peri-Iberian basins. Dispersal of *Calyptoria* stock was conditioned by the interplay of several factors, such as the tectonic framework, the development of epicontinental seas on both Tethyan margins, the early Toarcian transgression, the prevailing ocean current pattern, and their limited ability for dispersal. The revised chronostratigraphical framework of this dispersal episode reveals the coincidence with the thermal maximum recorded prior to the Early Toarcian Mass Extinction Event (ETMEE) in the westernmost Tethys Ocean. The concurrence of these factors played a significant role in the *Calyptoria* spreading, showing an inter-tropical distribution between 0º and 30º in both hemispheres. The taxonomical updating performed in the light of the current systematic trends support

ACCEPTED MANUSCRIPT

this adaptive strategy carried out by *Calyptoria* species, consisting of a sudden and practically synchronous dispersal without outstanding morphological changes instead of the diverse evolution of different brachiopod taxa in response to the environmental changes related to the ETMEE. Updating and rearranging of the species attributed to the genus *Calyptoria* suggest a new systematic scheme for several former attributions, supporting that lower Toarcian occurrences of *L. undulata* from westernmost Tethyan areas belong to *Calyptoria*, thus pointing toward the dispersal from the Northern peri-Gondwana seas to the westernmost Tethyan epicontinental platforms. Similar adaptive strategies were linked to other extinction events, supporting a possible pattern in the response of certain brachiopod populations to such biotic crises.

Keywords: Early Jurassic, thermal maximum, spiriferinides, faunal migration, adaptive strategies.

1. Introduction

Over the last decades, an interesting topic of discussion has drawn attention in relation to the Arab-Madagascan paleobiogeographical faunal affinities detected in several Early Jurassic platforms distributed worldwide and the timing of these influences. One of the most acknowledged spreading episodes was experienced by the necto-planktic biota of the so-called *Bouleiceras* fauna. The paleogeographical dispersion of these Arab-Madagascan ammonites took place in the early Toarcian, just prior the Early Toarcian Mass Extinction Event (ETMEE), revealing an immigration episode up to the Western Tethys Ocean (Mouterde, 1953, 1970, 1971; Dubar and Mouterde, 1953; Arkell, 1956; Geyer, 1965, 1971; Bizon et al., 1966; Dubar et al., 1970; Goy, 1974, 1975; Mouterde and Rocha, 1981; Goy et al., 1988; Goy and Martínez, 1996; Rulleau et al., 2003; Bardin et al., 2015), but also to the Panthalassa Ocean (Hillebrandt, 1973, 1984, 1987; Hillebrandt and Schmidt-Effing, 1981).

In this timespan, a distinctive and well-documented brachiopod fauna, mainly represented by spiriferinides, is usually recorded together with the classical *Bouleiceras* fauna in the North-Gondwana paleomargin and the Mid-East platforms. These spiriferinides were grouped into the genera *Spiriferina*,

ACCEPTED MANUSCRIPT

Liospiriferina, and *Calyptoria* (e.g. Thévenin, 1908; Alméras, 1987; Cooper, 1989; Alméras and Mouty, 2001; Chiocchini et al., 2002; Alméras et al., 2010; El-Sorogy et al., 2017). In contrast to the necto-planktic biota, brachiopods are strongly influenced by their brief larval dispersal stage and their epibenthic way of life. However, in several Western Tethys basins, the *Bouleiceras* fauna frequently occurs associated with spiriferinides comparable to those recorded in the Arab-Madagascan basins, commonly attributed to *Liospiriferina undulata* (Delance, 1969, Champetier, 1972; Rousselle, 1977; Calzada, 1981; Comas-Rengifo et al., 2006, 2013; García Joral et al., 2011; Baeza-Carratalá, 2013, Baeza-Carratalá et al., 2016a). So far, this brachiopod fauna has been overlooked as potential Arab-Madagascan immigrant fauna, as it is recorded mixed with the typical Western Tethyan communities.

The present work reveals, by assessing the brachiopod records and depositional environments in the North-Gondwana paleomargin and especially in the westernmost Tethyan areas, that Arab-Madagascan spiriferinides (representatives of the so-called *Calyptoria* stock herein) migrated in the same dispersal event as the *Bouleiceras* fauna, from the epicontinental peri-Gondwana seas to the neighboring Western Tethyan basins with similar environmental conditions, finding in the well-developed peri-Iberian platforms system a suitable habitat to establish stable communities.

The former attributions to *Calyptoria* and *Liospiriferina* of these forms have been revised evidencing a feasible dispersal pathway of *Calyptoria* mainly through the well-developed epicontinental platforms of the Western Tethys. For this purpose the most conspicuous and widely distributed occurrences of the index taxa of the *Calyptoria* stock are analyzed, performing a taxonomical updating in the light of the current systematic trends.

By tracking the pathway of this Arab-Madagascan brachiopods from the North-Gondwana paleomargin, present work infers a possible relationship between the global paleobiogeographic distribution of this fauna and depositional environments, also correlating the onset of its dispersal episode with an interplay of several global and regional factors, emphasizing the role played by a thermal maximum episode just prior to the ETMEE (García Joral et al., 2011; Gómez and Goy, 2011;

ACCEPTED MANUSCRIPT

Baeza Carratalá et al., 2015). This fauna, like all spire-bearing representatives did not survive to the global warming spike and environmental changes that occurred in the ETMEE boundary (Ager, 1987; Vörös, 2002; Comas-Rengifo et al., 2006; Baeza-Carratalá et al., 2015; Vörös et al., 2016, among others).

2. Materials and methods

Amidst the profuse Lower Jurassic outcrops prospected in the Iberian Range, Lusitanian Basin, and the Betic Range by the authors, only a few localities have exposed representatives of the genus *Calyptoria*. Present work performs a detailed morphometrical analysis on 58 specimens collected bed-by-bed in the localities of Ariño, Sot de Chera, Benifairó, Racó de Joana, Tarabillo y Fonte Coberta (Fig. 1), complemented by those figured by previous authors (Thévenin, 1908; Alméras, 1987; Cooper, 1989; Alméras and Mouty, 2001; Alméras et al., 2010) resulting in a total of 109 specimens analyzed.

The stratigraphic logs including the distribution of brachiopod assemblages to support the amalgamation between Arab/Madagascan and Iberian assemblages are shown in Figure 2. For the morphometrical analysis, the 90 specimens in whom the 8 biometric external parameters could be measured have been used (Fig. 3 and supplementary material). Subsequently, Principal Components Analysis (PCA) has been used as exploratory method for variable reduction (Hammer and Harper, 2006). This analysis was carried out by means of the PAST package (Hammer et al., 2001) using the variance-covariance matrix.

The internal structure of 3 individuals of *Calyptoria vulgata* was studied using the conventional method of taking acetate peels after making transverse serial sections. The distance between serial sections was 0.1 mm. High resolution microphotographs of acetate peels were taken using a Nikon CFI60 E600POL microscope. All specimens figured and acetate peels are deposited in the collections of the Earth and Environmental Sciences Department (University of Alicante, Spain) and the Paleontology Department (Complutense University of Madrid, Spain). The ammonoid

ACCEPTED MANUSCRIPT

chronostratigraphical zonal scheme is based on the standard zones proposed by Dommergues et al. (1997), Elmi et al. (1997), and Page (2003) for the Tethys Realm. Paleobiogeographic categorization of biochores follows the nomenclature proposed by Westermann (2000), subsequently adapted for the brachiopod fauna by several authors (e.g. Manceñido, 2002; Vörös, 2016).

3. Distribution and depositional environments of the *Calyptoria* lineage

In the early Toarcian, the East-African seaway began to open towards Madagascar (e.g. Ager, 1986; Ager and Sun, 1989, Geiger et al., 2004; Geiger and Schweigert, 2006), and an emergent Ethiopian brachiopod province was incipiently differentiated over Arabia-East Africa, with *Calyptoria* as characteristic taxon (Manceñido, 2002). The most conspicuous populations of this bioprovince are reported in Madagascar (Thévenin, 1908), South-Western Somalia (Chiocchini et al., 2002), Arabia (Alméras, 1987; Cooper, 1989; Alméras et al., 2010; El-Sorogy et al., 2017) and Syria (Alméras and Mouty, 2001). On the other hand, the well-established Euro-Boreal and Mediterranean brachiopod bioprovinces (Vörös, 2016), become less obvious in the early Toarcian due to the concurrence of diverse factors (Baeza-Carratalá, 2013), enabling the influence of this Arab-Madagascan fauna in the Western Tethys, whose presence has been documented in the Betic Range (Baeza-Carratalá, 2013; Baeza-Carratalá et al., 2016b), the Iberian Range (Rousselle, 1977; Comas-Rengifo et al., 2006; García Joral et al., 2011; Baeza-Carratalá et al., 2016a), the North-Eastern Iberian paleomargin (Delance, 1969; Calzada, 1981) and the Lusitanian Basin (Comas-Rengifo et al., 2013) (Fig. 4). A concise description of the depositional framework is summarized for each basin where *Calyptoria* is recorded to characterize the habitat preferred for its settlement.

3.1. Madagascar

The southernmost occurrences of *Calyptoria* correspond to the diverse and numerous populations from Western Madagascar. Thévenin (1908) included all these forms within the variability of

ACCEPTED MANUSCRIPT

Spiriferina rostrata var. *madagascariensis*, recorded in the *Bouleiceras* beds, mainly consisting of grayish claystone levels.

3.2. South-Western Somalia

In Southwestern Somalia, *Spiriferina madagascariensis* was recorded in the massive grey marls (1-3 m) of the upper member of the Uanei Fm., characterized by a relatively abundant fossil content, together with the *Bouleiceras* ammonite fauna (Chiocchini et al., 2002). This record is attributed to the Serpentinum Zone and was deposited in an outer ramp environment.

3.3. Arabian platforms

The record of the representatives of *Calyptoria* in the Arabian epicontinental platforms is widely recognized (Alméras, 1987; Cooper, 1989; Alméras et al., 2010; El-Sorogy et al., 2017). Cooper (1989) recorded the more diverse and extensive populations of *Calyptoria* and *Liospiriferina* in the Lower Marrat Fm., lower Toarcian in age, comprising mainly limestone and dolomite beds with several shale and calcareous quartz sandstone layers. The spiriferinide representatives of the *Calyptoria* stock seem to have found in Arabia a suitable area for diversification and the starting of its radiation, as these morphotypes led Cooper (1989) to split this stock into three nominal species of *Spiriferina* (each of them with a single specimen), two species of *Liospiriferina*, and also proposing the new genus *Calyptoria*, with two new species (based upon numerous specimens each).

Previously, Alméras (1987) had also recorded 485 specimens attributed to *L. undulata* derived from six outcrops in a Toarcian single bed at the bottom of the Middle Marrat Fm. (dated as belonging to the Serpentinum Zone) together with components of the *Bouleiceras* fauna. They were recorded in a transitional environment between continental sandy facies and infralittoral deposits, specifying subsequently this depositional setting (Alméras et al., 2010) as the middle part of the infralittoral

ACCEPTED MANUSCRIPT

environment with grey/yellowish bioclastic dolomite limestone beds. This environment is in accordance with the shallow epicontinental platforms where *Calyptoria* is usually recorded.

The stock of *L. undulata* recorded by Alméras (1987) evidences a great variability in size, folding pattern and beak features. This variability led to subsequent splitting of the material formerly attributed to *L. undulata* into several taxa belonging to *Liospiriferina* (e.g. *L. vulgata, L. obesa*) and *Calyptoria* (Alméras et al., 2010).

3.4. Syrian platform

Alméras and Mouty (2001) recorded abundant specimens of *L. undulata* attributable to *Calyptoria* together with some species of zeillerides in the Treize Fm. This lithostratigraphical unit was deposited in a shallow marine platform and consists of yellowish thinly interbedded limestone and marl beds dated within the lower Toarcian Madagascariensis Zone.

3.5. Betic Range

In the Betic Range, representatives of *Calyptoria* are recorded in the earliest Toarcian from the epioceanic Subbetic area (Baeza-Carratalá, 2008, 2013) and in the transitional Prebetic-Subbetic zones (La Mola region, Baeza-Carratalá et al., 2016b). In the Subbetic domain, the uppermost Pliensbachian-lowermost Toarcian sediments are mainly represented by the Zegrí Fm., made up by alternating yellowish and greenish marls and marly limestone, with sporadic levels of yellowish sandy marlstones at the bottom (Fig. 2). Otherwise, La Mola region is considered an intermediate area between shallow epicontinental platforms which prevailed in the Prebetic on the North and, southwards, the Subbetic domain characterized by pelagic seamount facies. In this area, yellowish marls and interspersed marly limestone beds (Fig. 2), comparable to the Subbetic area, characterize the lowermost Toarcian deposits as well (Baeza-Carratalá et al., 2016b).

ACCEPTED MANUSCRIPT

Populations in these mainly epioceanic (and transitional) domains consist of scarce occurrences of *L. undulata* (Subbetic: six specimens from two nearby outcrops; La Mola: three specimens from a single outcrop) with low median fold and occasionally obscurely ribbed (or capillate) flanks.

3.6. Ibero-Levantine Sector (ILS) of the Iberian Range

This region (E-Spain) comprises the southernmost Jurassic outcrops of the peri-Iberian epicontinental platforms. Representatives of *Calyptoria* in this area are recorded in three localities (Racó de Joana, Benifairó-D, and Sot de Chera, see Fig. 2), within the Turmiel Fm., which consists of an alternation of well-bedded grey/yellowish marls and mudstone beds arranged into deepening and shallowing-upwards sequences (Gómez and Goy, 2000). These marly facies are deposited between the red bioclastic grainstone-packstone beds of the Upper Pliensbachian-lowermost Toarcian Barahona Fm. and the Middle-Upper Toarcian Casinos Fm., this latter unit mainly consisting of grayish mudstone/wackestone beds with marly levels interspersed. The recorded populations include around a hundred individuals attributed to *L.*? *undulata*, showing high intraspecific variability in shape and size (Baeza-Carratalá et al., 2016a).

3.7. Central and Northern Iberian Range

In the innermost areas of the Iberian Range, representatives of *Calyptoria* assigned to *L. undulata* are recorded in the lower Toarcian Semicelatum Subzone and in the lowermost Elegantulum Subzone (Goy et al., 1984; García Joral and Goy, 2000, García Joral et al, 2011) in several outcrops of the Aragonese branch, i.e.: Rambla del Salto, Ariño, Obón, and Calanda (Rousselle, 1977; Arias et al., 1992; Comas-Rengifo et al., 1996; Colás, 2008). They show high variability in morphotypes, ranging from sharper to wider median fold. They also occur in the Turmiel Fm., which consists of an alternation of micritic mudstone and marl/marly limestone (Fig. 2) deposited in a shallow

ACCEPTED MANUSCRIPT

epicontinental platform. In contrast, this species has never been recorded in the Castilian Branch or in the Northwestern sector of this range.

3.8. North-Eastern Iberian Paleomargin

Liospiriferina undulata is also recorded in the pre-Pyrenees constituting the northernmost record of *Calyptoria*. In outcrops near Camarasa, Delance (1969) and Calzada (1981) recorded very few specimens in a lithostratigraphical framework comparable to that of the Iberian Range. They occur in yellowish siltstone with more calcareous levels interspersed. The morphotype typical of these outcrops shows a rather acute dorsal median fold. Calzada (1981) assigned this material to the early Toarcian (and latest Pliensbachian, with doubts).

3.9. Lusitanian basin

This region represents the westernmost occurrence of the *Calyptoria* stock. In the San Giao Fm. of the Fonte Coberta section, Comas-Rengifo et al. (2013) recorded two specimens of *L*.? aff. *undulata* in the lowermost Levisoni Chronozone, just prior to the ETMEE. They come from the whitish grey marls beds corresponding to a shallow to hemipelagic depositional environment (Fig. 2).

4. Biostratigraphic record of *Calyptoria*

The biostratigraphic range of the *Calyptoria* representatives in the Western Tethys was difficult to establish precisely until relatively few years ago. Most of the constituents from this stock were formerly assigned to the Upper Pliensbachian (Spinatum Zone)–Lower Toarcian (Serpentinum Zone) interval, depending on the authors. However, a more accurate calibration has been achieved by the finding of representatives of the Family Hildoceratidae (*Bouleiceras* and *Protogrammoceras*) in the sub-Mediterranean ammonoid Bioprovince (Page, 2003), revealing a remarkable record in the central

ACCEPTED MANUSCRIPT

and southern areas of the Iberian Range, also associated with *Dactylioceras* (*Orthodactylites*), or some other Hildoceratidae, such as *Eleganticeras*, *Harpoceras* or *Hildaites*.

Hence, the research line carried out over the last decades on westernmost Tethyan ammonoids allows better understanding the biostratigraphic distribution of the species belonging to the aforementioned genera (Goy and Martínez, 1996; Goy et al., 1997; Gómez and Goy, 2011) dismissing the assignment of the Iberian *Bouleiceras* to the Upper Pliensbachian, as asserted by Geyer (1965, 1971), Behmel and Geyer (1966), and Bizon et al. (1966), but also ruling out that its record is exclusively restricted to the lower Toarcian Serpentinum Zone (Mouterde, 1970, 1971; Dubar et al., 1970).

In the Ibero-Levantine sector of the Iberian Range, some previous authors such as Bizon et al. (1966, p. 902; pl. 27a, 7a-c) reported the presence of *Bouleiceras nitescens* (Thèvenin) together with a brachiopod assemblage comprising spiriferinides now attributed to *Calyptoria vulgata* (Cooper) and some foraminifera in the upper part of the Spinatum Zone. This assemblage comes from level 7 (being about 6 m thick) of the Racó de Joana section and includes *Dispiriferina*? *oxyptera* (Buvignier), *Lobothyris arcta* (Dubar) and *Aulacothyris iberica* Dubar. The brachiopod fauna of this outcrop was updated by Baeza-Carratalá et al. (2016a) and these species typify the Tenuicostatum Zone in the peri-Iberian platforms (Mouterde, 1971; Alméras and Fauré, 2000; García Joral and Goy, 2000; García Joral et al., 2011). The distribution of the genus *Bouleiceras* comprises the chronostratigraphic interval corresponding to the Tenuicostatum/Polymorphum and Serpentinum/Levisoni chronozones of the of NW-European and Mediterranean provinces respectively (*sensu* Elmi et al., 1997; Page, 2003). This genus occurred in most of the localities together with *Calyptoria* and its origin should be acknowledged in the latest Pliensbachian Hildoceratidae showing evolute, tuberculate, and ribbed forms with bouleiceratitic suture (Guex, 1974). They are likely derived from Arieticeratinae representatives, such as *Canavaria* or *Tauromeniceras*, which may present tubercles at both ends of the ribs. *Bouleiceras* representatives are frequent in the Sub-Mediterranean (Iberian Range and Portugal) and Mediterranean

ACCEPTED MANUSCRIPT

(Sicily, Apennines, Betic Range, North-Africa, Arabia, and Madagascar) provinces. According to the known record, the oldest species assigned to *Bouleiceras* is *B. chakdallaense* Fatmi, which comes from the Middle Member of the Datta Fm. (NE-Pakistan) and shows remarkable affinities with *B. elegans* Arkell recorded in Madagascar, Arabia and Spain, where it does not exceed the upper boundary of the Tenuicostatum Zone. A single specimen of *B. chakdallaense* was recorded from Chile in levels corresponding to the Tenuicostatum Zone, Simplex Subzone (Hillebrandt and Schmidt-Effing, 1981), which is equivalent to the lower part of the Sub-Mediterranean Tenuicostatum Zone. Interestingly, *Canavaria* and *Tauromeniceras* are also present in the Andean region (Hillebrandt, 2006; Riccardi et al., 2011).

Another bituberculate species in the inner whorls of the flanks is *B. nitescens*, which was also recorded in the Middle Member of the Datta Fm. from NE-Pakistan. The first record of this species in Madagascar and Arabia is imprecise but its occurrence in equivalent levels to the Sub-Mediterranean Tenuicostatum Chronozone, Semicelatum Subchronozone cannot be dismissed. On the other hand, the finding in Arabia of a rich ammonite fauna with *Bouleiceras* and *Protogrammoceras madagascariense* (Thévenin) at the bottom of the Middle Marrat Fm. (Enay and Mangold, 1994; Alméras et al., 2010), does not justify its attribution to the Serpentinum Zone, since both taxa have been found associated to *D.* (*O.*) *semicelatum* (Simpson), below the first record of *Eleganticeras*, in levels corresponding to the Tenuicostatum Chronozone (Semicelatum Subchronozone).

In the peri-Iberian platforms, the oldest record corresponds to *Bouleiceras* sp. (a closer form to *B. elegans*) that occurs in the Central Sector of the Iberian Cordillera in the Tenuicostatum Zone, Semicelatum Subzone (Herrero, 1993). This species, as well as *B. arabicum* Arkell and *B. marraticum* Arkell have not been found above the Semicelatum Subzone. Other species such as *B. nitescens*, *B. tumidum* Arkell and *B.* sp. nov., have been recorded in the uppermost Tenuicostatum Zone and in the lowermost Serpentinum Zone and they were not significantly affected by the ETMEE at the

ACCEPTED MANUSCRIPT

Tenuicostatum-Serpentinum boundary which also involved ammonoids (Cecca and Maccioni, 2004; Gómez and Goy, 2011).

Accordingly, in the Iberian Range, the genus *Bouleiceras* has been recorded in the Semicelatum Subzone, in younger levels than those attributed to *B.* cf. *chakdallaense* in Chile, but there are also some specimens derived from the Serpentinum Zone, Elegantulum Subzone (Mouterde, 1971; Goy, 1974; Goy and Martínez, 1996). The same occurs with some specimens recorded from the Serpentinum Zone of Tomar, Portugal (Mouterde and Rocha, 1981). Consequently, it can be stated that *Bouleiceras* have not been recorded above the Elegantulum Subchronozone in the peri-Iberian platforms system.

Calyptoria is also commonly recorded together with *Protogrammoceras madagascariense* in the Indo-Madagascan region and in the peri-Iberian basins. This ammonoid shows a bit earlier record than the earliest *Bouleiceras*, as can be evidenced in Madagascar (Blaison, 1968), and persists up to the lowermost Elegantulum Subchronozone. Cooper (1989) reported also *Liospiriferina obesa* from Central Arabia higher up in the Marrat Fm., in a single station with *Nejdia bramkampki*, late Toarcian in age. In our opinion, this record has to be corroborated, as it is younger to any other record of the genus and to the extinction boundary of the spiriferinides in other regions.

5. Spiriferinides as the main faunal components of the *Calyptoria* stock

The episode of the pervasive colonization led by the Arab-Madagascan *Bouleiceras* fauna is reported in the North-Gondwana paleomargin and the Western Tethyan basins together with the occurrence of spiriferinides with a rather stable and regular external shape, consisting of morphotypes with a conspicuous dorsal median fold and often faintly or obscurely ribbed on the flanks. These morphotypes were attributed to different taxa, depending on the basin, prevailing the assignments into *Liospiriferina undulata* and *Calyptoria* spp. Morphometrical analyses of taxa in the widely distributed occurrences of the *Calyptoria* stock is performed including, in addition to *L. undulata,* some species closely related to *Liospiriferina,* the Madagascan *Spiriferina madagascariensis* Thévenin, 1908 and

ACCEPTED MANUSCRIPT

several species of *Calyptoria* Cooper, 1989. This taxonomical updating is required to reassess the former attributions to *Calyptoria* and *Liospiriferina* in the Arab-Madagascan domain, testing therefore the hypothesis of a feasible dispersion of this brachiopod fauna to the well-developed epicontinental seas of the Western Tethys.

5.1. Morphometrical analysis.

Principal components analysis (PCA) simplifies the visualization and comparison of morphological variability within the group. The first two principal components obtained by the PCA performed (PC1 and PC2) explain 90% of the variance within the data (Fig. 5, Table 1), and have accordingly been considered as representing the variability within the group. The PCA3 values do not provide any improvement in discrimination of sets. In the Figure 5A, the vectors of the dimensions have been superposed to the PCA scatter plot, showing that PC1 reflects mainly a size-related distribution, as usual in this kind of dimensional analysis, whereas the second component separates the specimens mainly by their relative thickness and folding pattern, i.e. thicker morphotypes and a higher folding pattern acquire more positive values on PC2, whereas wider/larger morphotypes and a lower folding pattern have negative values along this axis. Another significant discriminating factor is the relative position of the maximum width along the shell-length. Thus, specimens with the maximum width shifted toward the anterior margin score more negative values along this axis.

In the Figure 5B, specimens are clustered considering the region where they were recorded, showing a different occupation of morpho-space though with limited degree of overlapping in certain narrow areas. The Madagascan individuals are distributed mainly in the lower right quadrant of the plot (positive values along PC1 and negative values along PC2); the Arabian records are distributed in the upper left sector, and the Iberian ones in the lower left sector. This distribution suggests a geographical discrimination of species or morphotypes (Fig. 5C).

ACCEPTED MANUSCRIPT

Results of this analysis also display the high morphological variability of the Madagascan specimens. This cluster shows some morphotypes (including the type of *S. madagascariensis*) distributed in the extreme of the variation range of the sample, and others more linked to the Arabian or Iberian morphologies. On the other hand, it is also noteworthy that the values scored by the type of *S. undulata*, Seguenza from Sicily, are clearly located morphologically distant from the other populations under study.

5.2. Analysis of the internal features on *Calyptoria vulgata*

The internal structure of the genus *Calyptoria* is poorly known. Only partial sections on *Liospiriferina undulata* were made by Rousselle (1977), lacking most of the data relating to the anterior part of the shell, including spiralia. The internal features of this genus are now revealed on the basis of three Iberian specimens (Figs. 6-8) previously attributed to *L. undulata* (*Calyptoria vulgata* herein).

Calyptoria vulgata displays umbonal lateral cavities with a rounded triangular section. Pedicle collar is well-developed. A high ventral median septum persists up to 3/4 of shell length, with a slender tichorhinum detected in the mid-length. Dental plates are subparallel to slightly convergent dorsally and somewhat arcuate. Hinge teeth are strong and massive, interlocked in narrow sockets which acquire wider expansion anteriorly. Slight denticula are present. Outer and inner socket-ridges are well-developed. Cardinal process is a short, depressed and highly striated ctenophoridium on a low and massive cardinal platform and a slender but well-differentiated myophragm.

Dorsal median septum is low. Hinge plates are clearly tilted towards the dorsal valve, showing crural bases with a lamellar section and dorsally inclined. Jugum is well-developed and slightly wrinkled. Cone-shaped spiralia with subparallel, laterally oriented, development of spires. Each spiralium consists of 12-14 whorls equally occupying both dorsal and ventral cavities, with the coiling axis subparalell to the articulation plane.

ACCEPTED MANUSCRIPT

6. Discussion

6.1. The question of *Spiriferina undulata* Seguenza, 1885 and the initial diagnosis of the genus *Calyptoria* Cooper, 1989.

Since Seguenza (1885) erected the species *Spiriferina undulata* from the "*rocche rosse presso Galati*" in North-East Sicily, this species has acquired a catch-all status to denote several spiriferinides, sometimes smooth, sometimes faintly ribbed, with a clear dorsal median fold round-shaped in outline. Attributions to the species *undulata* are widely reported in the Arabian Platform and the westernmost Tethyan areas with a variety of generic assignments such as *Liospiriferina* (Rousselle, 1977; Calzada, 1981; Alméras, 1987; García Joral and Goy, 2000; Alméras et al., 2010; Baeza-Carratalá, 2013; El-Sorogy et al., 2017); *Callospiriferina*? (Comas-Rengifo et al., 2006), or under more open nomenclature (*Liospiriferina*?; Baeza-Carratalá, 2008, Baeza-Carratala et al., 2016a; even refining the attribution as *Liospiriferina? undulata* (Seguenza) *sensu* Rousselle (1977), *vid* García Joral et al., 2011).

To this taxonomic uncertainty, the clear resemblance of the different aforementioned attributions with the stock of *S. madagascariensis* Thévenin, 1908 and representatives of the genus *Calyptoria*, should be added, even taking into account that some of the former assignments to *L. undulata* (Alméras, 1987) were later amended and allocated to the genus *Calyptoria* (Alméras et al., 2010).

A further challenging topic is the ambiguous diagnosis of *Calyptoria* as was erected by Cooper (1989): "spiriferacean with smooth shell surface, obscurely costate in the flanks". The diagnosis was based on the obscure lateral costation, emphasizing the absence of spines or granules which separate this genus from *Liospiriferina*. Cooper (1989) did not show the internal structure of this genus, only giving some occasional data such as a large ventral median septum, wide sockets and short septal plates.

As can be deduced from the morphometrical analysis yielded by the PCA (Fig. 5), the species *Spiriferina undulata* Seguenza, 1885 is detached from the Arab-Madagascan and westernmost Tethyan stocks and thus cannot be considered as a constituent of these lineages. This proposal was somehow

ACCEPTED MANUSCRIPT

foreseen by Vörös (2009), who considered Seguenza´s species within the synonymic list of *Liospiriferina sicula* (Gemmellaro, 1874). In the current reappraisal, we also assume that the Sicilian species can be regarded as member of the group *L. obtusa* (Oppel, 1861) - *L. sicula* (Gemmellaro, 1874), widely recorded in the Mediterranean bioprovince. Actually, some previous authors noticed the affinity of these taxa proposing combinations such as *Spiriferina obtusa undulata* in the material from Greece in the case that several subspecies were validated for the *L. obtusa* group (Manceñido, 1993). In addition, it should be borne in mind that the Mediterranean stock of the former *S. undulata* might be older than the Arab-Madagascan fauna. In this sense, Seguenza's material (1885) is recorded together with an ammonite fauna mostly Lower-Upper Pliensbachian in age, in line with the common occurrences of *L. sicula-L.obtusa* group in the Mediterranean localities.

Furthermore, if we strictly consider the initial diagnosis of *Calyptoria* (without pustules or spinules), the *L. undulata* stock cannot be included into this genus since microgranules or spines are clearly visible on their entire surface (Fig. 9). Nevertheless, updated reassessments of some species formerly fitted in *L. undulata* (noticeably microornamented) have been transferred to *Calyptoria* overlooking this feature and emphasizing some other attributes (Alméras et al., 2010). On the other hand, all the representatives of the Subfamily Spiriferininae Davidson, 1884 are unmistakably microornamented except for *Calyptoria* as defined by Cooper (1989). It is therefore expected that Cooper (1989) more than likely may have dealt with decorticated specimens, as it happens in the Iberian material where microspinulose specimens and those without ornamentation clearly coexist in the same levels, depending on the state of preservation of the external layers of the shell (cf. Figs. 9.6, 9.10, 9.12).

On the other hand, the generic synonymy of *Calyptoria* has also been debated by other previous authors (see Pozza, 2001 for discussion in this sense). Consequently, amending the diagnosis of *Calyptoria* is desirable. This strengthens in latest works (He et al., 2015) in which a new arrangement for the Superfamily Spiriferinoidea is displayed through parsimony analysis, attaching relevance to a total of 20 internal/external characters coded in all genera belonging to this superfamily. He et al.

ACCEPTED MANUSCRIPT

(2015) placed *Calyptoria* Cooper, 1989 within the Subfamily Spiriferininae Davidson, 1884, together with *Spiriferina* d'Orbigny, 1847 (a clearly microornamented genus), while *Liospiriferina* Rousselle, 1977 is split from these genera and reorganized within the Subfamily Qinghaispiriferininae He and Chen, 2015, together with *Qinghaispiriferina* Sun and Ye, 1982.

With respect to the internal structure of *Calyptoria* (Figs. 6-8), it can be deduced that lower Jurassic representatives of the Superfamily Spiriferinoidea Davidson, 1884 show comparable internal architecture, but analyzing the small number of previous works including serial sections with spiralium data, several features can be used as generic diagnostic criteria. Thus, *Calyptoria* differs from *Cisnerospira* Manceñido, 2004 because this latter genus displays dental plates slightly divergent dorsally, short hinge plates nearly fused to the socket ridges, crural bases very close (even attached) to the dorsal valve, dorsal median septum absent, and spiralium probably oriented ventrally up to posteriorly (Baeza-Carratalá et al., 2016c). On the other hand, *Liospiriferina* (probably the genus closest to *Calyptoria*) shows notably shorter ventral median septum, which instead persists up to 3/4 of shell-length in *Calyptoria*. Referring to the spiralium, *Liospiriferina* reveals spiralia with divergent, ventrally oriented, apices (except for *L. semicircularis* Böse, *vid* Rousselle, 1977). In this sense, *Calyptoria* better resembles some Triassic representatives of Spiriferinoidea such as *Triadispira* Dagys, 1961 or *Viligella* Dagys, 1965, showing spiralia laterally oriented, subparallel to commissure plane.

6.2. Systematic scheme for the constituents of the *Calyptoria* lineage

Concerning the aforementioned question, and at a previous standpoint, thus far without knowledge about internal structure of *Calyptoria* to refer to and to compare with, one wondered which were the proper diagnostic criteria to update the species belonging to the *Calyptoria* complex? The analysis carried out in this study provides new data based on a) serial sections performed in three specimens with different external morphotypes of the former *L. undulata* (updated as *Calyptoria vulgata*) to elucidate the internal structure of the group; b) statistical approach through morphometrical analyses in

ACCEPTED MANUSCRIPT

a dataset including all nominal species. Having in mind the taxonomical proposal by previous authors and the morphological distinction depending on the geographical provenance of the specimens analyzed (Fig. 5B), the *Calyptoria* complex can be systematically arranged in distinct species as follows (Fig. 5C).

- The Madagascan specimens originally attributed to *Spiriferina madagascariensis* should maintain this specific denomination combined as *Calyptoria madagascariensis*.. From the PCA analysis shown in figure 5, it could be inferred that one specimen (figured by Thevenin, 1908, plate 5, fig.2) can be adscript to *C. vulgata* and other one (Thevenin, 1908, plate 5, fig. 9) to *C. obesa*. However, in absence of more extensive populations to study its variability, it seems preferable do not introduce more nomenclatorial noise based in a single specimen, and maintain all Malagasian specimens together within the same attribution. This species can be considered ancestral to the group and consequently can show high intraspecific variability. The specimen figured by Thévenin (1908, Pl. 5, fig. 3-3b) considered as a typical morphology by this author is herein designated as the lectotype of the species.

- The new species of *Liospiriferina* (*L. obesa* and *L. vulgata*) erected by Cooper (1989) in Arabia should be reassigned to the genus *Calyptoria* retaining their specific designation (*Calyptoria obesa* and *C. vulgata*), whereas the diagnostic criteria used to differentiate the former species of *Calyptoria* erected by Cooper (*C. extensa* and *C. carinata*) seem to be more inconsistent and the same specific assignation (*Calyptoria extensa*) is preferable to encompass both forms. The assignations to the Cooper's species by Alméras et al. (2010) have been reorganized on the basis of the PCA scores of the figured specimens in the morphometric analysis (Table 2).

- The Syrian specimens described as *L. undulata* by Almèras and Mouty (2001) should be included in *Calyptoria vulgata*, after their arrangement in the PCA scatter plot (Fig. 5).

- The Iberian and Portuguese specimens are close to the type of *C. vulgata* and they deserve to be included within the variability of this species. In the peri-Iberian basins, *C. vulgata* develops very

ACCEPTED MANUSCRIPT

homogeneous populations distributed in a few stratigraphical levels, although including some more globose and highly plicate forms which can be considered in the extreme range of variability of this species, close to *C. obesa*. The morphological variability of *C. vulgata* in the peri-Iberian basins is shown in Figure 9.

- Finally, the type of *L. undulata* (Seguenza) is located in the PCA scatter plot clearly unrelated with the morpho-space occupied by the analyzed specimens, suggesting a different taxonomical assignment.

As a result of this taxonomic scheme, the synonymic list of the species now attributed to *Calyptoria* is updated as summarized in Table 2.

6.3. Paleobiogeography of the *Calyptoria* association

6.3.1. Factors influencing the Calyptoria association paleobiogeography

In the Early Toarcian, the distribution of diverse brachiopod groups through the North-Gondwana paleomargin and the Western Tethys Ocean was influenced by interplay of different factors:

(a) Tectonics and ocean currents pattern played an important role in the distribution of biochoremas. In the North-Gondwana paleomargin, the East-African seaway began to open towards Madagascar as stated previously in this paper, and an emergent Ethiopian brachiopods bioprovince was incipiently differentiated over Arabia-East Africa, with *Calyptoria* among the endemic taxa (cf. Cooper, 1989; Manceñido, 2002) (Fig. 4). Likewise, the opening of the Atlantic Ocean started across the Hispanic Corridor (Manceñido, 1990, 2002; Manceñido and Dagys, 1992; Damborenea, 2000; Aberhan, 2001; Sha, 2002; García Joral et al., 2011) connecting Neo-Tethys Ocean with the Pacific Realm, while the Viking Straits (Poulton and Callomon, 1977; Callomon, 1979) allowed communication with the Arctic region along the "Laurasian Seaway" (Bjerrum et al., 2001). Otherwise, a northern Tethyan seaway across the peri-Laurasian epicontinental platforms was developed latter allowing for a wide spreading

ACCEPTED MANUSCRIPT

of brachiopod fauna along the northern margin of the Tethys Ocean (cf. Baeza-Carratalá and Sepehriannasab, 2014).

(b) Sea-level fluctuations definitely affected the provinciality in the Western Tethys and the well-established Euro-Boreal and Mediterranean bioprovinces become lesser evident probably due to the major Early Toarcian marine transgression (Hallam, 2001; Rulleau et al., 2003; García Joral et al., 2011, Dera et al., 2011; Andrade et al., 2016), enabling unification of faunas and disruption of biochoremas not only for brachiopod fauna (cf. García Joral and Goy, 2000; Baeza-Carratalá et al., 2016b), but also other marine biota (cf. Rulleau et al., 2003; Macchioni and Cecca, 2002; Damborenea, 2002; Dera et al., 2011), evidencing the Arab-Madagascan occurrences in the Western Tethys (Fig. 4).

(c) The Pliensbachian-Toarcian transition was a period of changes in long-term environmental conditions leading up to the well-known main crisis event (ETMEE) especially severe for the benthic biota (cf. Harries and Little, 1999; Dera et al., 2011, Suan et al., 2010, Gómez and Goy, 2011). Diverse environmental changes triggered several perturbations on sea-water temperatures affecting brachiopod fauna (García Joral et al., 2011; Gómez and Goy, 2011; Baeza-Carratalá et al., 2015; Gómez et al., 2016) contributing to extinction, turnovers and/or migration in several groups (cf. Vörös, 2002; García Joral et al., 2011; Baeza-Carratalá et al., 2015, 2017; Vörös et al., 2016).

6.3.2. Starting homeland, proliferation and dispersal of the Calyptoria association

Taking into account the aforementioned paleogeographical and environmental context outlined above, the chronostratigraphic data, and analyzing the PCA distribution of the representatives of this stock (Figs. 5, 10), we can assess the systematic arrangement proposed in terms of several clusters representing a biogeographical pattern. Cluster 1 corresponds to the Madagascar fauna, suggesting the place where *Calyptoria* established its original homeland. The starting point of this stock is represented by *C. madagascariensis* with a great intraspecific variability (Thévenin, 1908), which is usual in pioneer populations occupying a vacant benthic ecospace, as can be deduced from the oligotypic

ACCEPTED MANUSCRIPT

assemblages reported by previous authors in Madagascar and the Arabian-Syrian platforms (Thévenin, 1908; Alméras, 1987; Cooper, 1989; Alméras and Mouty, 2001; Alméras et al., 2010; El-Sorogy et al., 2017).

Cluster 2 consists of the Arabian fauna. In this platforms system, *Calyptoria* established stable populations conducting a radiation led by *C. madagascariensis* itself, as can be interpreted by the narrow overlapping area between Clusters 1 and 2 (Fig. 5B). Starting from the high variability of *C. madagascariensis*, the diversification in Arabia gave rise to three different species: *C. obesa, C. extensa,* and *C. vulgata*. Only this latter species spread westward towards Syria and the Western Tethys platforms around Iberia (Cluster 3).

Thus, the community settled in the well-developed peri-Iberian epicontinental platforms system by means of *C. vulgata* (Cluster 3), which became mixed with the well-established NW-European populations therein developed showing occasional occurrences in shallower areas of the deeper Mediterranean Bioprovince (Subbetic and La Mola region) (Figs. 1, 10). These Subbetic epioceanic platforms and transitional ramps did not constitute filter-barriers but rather facilitated brachiopod dispersal enabling faunal mixing and exchange between epicontinental/epioceanic environments (Baeza-Carratalá et al., 2016b).

Finally, the position of the Seguenza's material from Sicily in the overall display of PCA (Fig. 5) can be interpreted as an evidence of the paleobiogeographical disconnection of this species with the Arab-Madagascan stock, thus representing an Eastern (and probably ancient) counterpart belonging to the Mediterranean *Liospiriferina sicula-obtusa* group.

6.3.3. Epicontinental environments and thermal maximum prior to the ETMEE as aids to the Calyptoria dispersal

Analyzing facies distribution and habitats throughout the occurrences of *Calyptoria*, it can be deduced that this lineage settled in the shallow epicontinental platforms of the peri-Gondwana

ACCEPTED MANUSCRIPT

paleomargin and the peri-Iberian epicontinental platforms of the westernmost Tethys Ocean, in a depositional environment frequently with high terrigenous input associated to transgressive sedimentation (Fig. 4). It is well-known that brachiopod dispersal is quite restricted due to their short larval stage. Owing to this limitation, *Calyptoria* only reached the closest comparable habitats to the Arab-Madagascan platforms (its original homeland) in the westernmost Tethyan areas, where a well-developed system of epicontinental platforms was distributed around the Iberian Subplate in the Early Jurassic (Gómez and Goy, 2005). This dispersal was determined by the inferred prevalent oceanic current pattern westward (Bjerrum et al., 2001). This clockwise pattern was also previously inferred for several brachiopod groups in the Western Tethys (Ager and Walley, 1977; Vörös, 2002; Baeza-Carratalá and García Joral, 2012; Baeza-Carratalá et al., 2015).

The link between both epicontinental margins was also promoted by the latest Pliensbachian-early Toarcian sea-level rise, which triggered unification of biochoremas and free connection among basins, hence reducing local endemism in the brachiopod fauna (cf. Baeza-Carratalá, 2013). Thus, the well-established peri-Gondwana stock of *Calyptoria* reached in its dispersal the peri-Iberian platform system, being the epioceanic areas of the Mediterranean bioprovince (Baeza-Carratalá, 2013; Baeza-Carratalá et al., 2016b) just a passageway where this fauna did not establish enduring populations, as can be deduced from the very scarce occurrences in these areas (Fig. 10).

Due to the environmental conditions that specially determine the brachiopods settlement, it can be inferred that *Calyptoria* representatives were looking for, in their spreading route, epicontinental seas characterized by shallow and oxygenated habitats with nutrients availability, high terrigenous inputs and, probably as main factor, equatorial temperature ranges. The main hypothetical controlling factor might thus be temperature. The Mediterranean province was deeper and consequently colder than the NW-European epicontinental seas and therefore was not a suitable habitat for *Calyptoria*, coming from warmer Arab-Madagascan seas distributed at very low paleolatitudes. Significantly, global distribution

ACCEPTED MANUSCRIPT

of *Calyptoria* appears to be confined to the warmer shallow seas developed in both hemispheres, between 30ºN–30ºS (Fig. 4).

Moreover, the dispersal of *Calyptoria* coincides with a major early Toarcian warming interval recorded in the Western Tethys embracing a thermal maximum just prior to the ETMEE. The beginning of the *Calyptoria* dispersal was concurrent with the onset of a progressively warmer climate (Fig. 10). After the well-known Pliensbachian cooling, paleotemperatures reached in the inner part of the Iberian platform system an average of 16.3 °C in the Tenuicostatum Zone, representing an increasing seawater temperature in the order of 4–5 °C (Gómez and Goy, 2011; García Joral et al., 2011; Gómez et al., 2016). The thermal maximum reached average of 23º C in the central part of these epicontinental seas implying a rising of temperature about 6.7 °C around the Tenuicostatum-Serpentinum zonal boundary. The main spreading event just coincided with this thermal maximum. In the Iberian Range, occurrence of *Calyptoria vulgata* is restricted to a few strata (Fig. 2), just prior to ETMEE (cf. Gómez and Goy, 2011; García Joral et al., 2011; Baeza-Carratalá et al., 2015, 2016a), as well as in the very last level prior to ETMEE in the Lusitanian Basin (Comas-Rengifo et al., 2013).

Consequently, it can be inferred that, in the Iberian platforms, this stock did not experience an episode of continuous radiation, speciation, or evolutionary adaptation during the Pb-To extinction interval, as other spiriferinide representatives evidenced, such as the *L. falloti-L.rostrata* group, showing noticeable size-change trends (García Joral et al., 2011, 2015, Baeza-Carratalá et al., 2017). *Calyptoria* occurred in a particularly specific time, and generally with comparable body size and minor morphological adaptations, which agrees with the fact that the environmental conditions that prevailed around Iberia (mostly referred to epicontinental and warmer shallow seas) were analogous to those of its Arab-Madagascan homeland.

Summarizing, it can be inferred that the interplay of the short larval stage, the prevailing currents pattern during Toarcian, relatively high sea level and latitudinal paleotemperatures control were the constraints which favored the dispersal of *Calyptoria* representatives into the Neo-Tethys Ocean, since

ACCEPTED MANUSCRIPT

they could not migrate across the large Hispanic Corridor seaway or the Viking straits and the East-African seaway southward, likely due to the cooling of the seawater in higher latitudes. Members of *Bouleiceras* fauna were likewise distributed in low latitudes, probably depending on the same thermal control (Fig. 4). The record of this cephalopod genus in the Eastern Panthalassa Ocean is not accompanied by reports of representatives of *Calyptoria* (e.g.: Hillebrandt, 1973, 1984, 1987; Hillebrandt and Schmidt-Effing, 1981), as a consequence of the much greater dispersal capability of ammonites. A comparable latitudinal brachiopod dispersal invoking as controlling factors prevailing currents pattern, development of new favorable habitats, and a global warming event prior to extinction, and similarly related to a mass extinction event (the end-Ordovician one) has been previously reported by Colmenar (2015).

6.4. Integration with the Western Tethyan communities and extinction

Upper Pliensbachian-Lower Toarcian brachiopods have been widely reported in the peri-Iberian platform system (e.g. Calzada, 1981; García Joral and Goy, 2000; Comas-Rengifo et al., 2006, 2013; García Joral et al., 2011; Baeza-Carratalá, 2013, Baeza-Carratalá et al., 2016a, among others). The analysis of the assemblages and their relationship with depositional sequences was crucial to advance on their ecological and paleobiogeographical affinities. Thus, García Joral and Goy (2000) early foresaw an amalgamation of two subsets with different biogeographical connotations in the assemblages typifying the Tenuicostatum Zone. The first one was widely-distributed throughout the Euro-Boreal epicontinental seas and the second one was "more endemic". Subsequently, García Joral et al. (2011) inferred a latitudinal/climate gradient related to the progressive replacement of both stocks, being the first one more adapted to cooler conditions, and the second assemblage, with *L. undulata* (*Calyptoria vulgata* herein), better adapted to warmer environments. These authors suggested that the latter assemblage replaced the first widely-distributed stock when a warming period started in the early Toarcian Tenuicostatum Zone. Similar amalgamations were reported in several works (Bizon et al.,

ACCEPTED MANUSCRIPT

1966; Champetier, 1972; Comas-Rengifo et al., 2013; Baeza-Carratalá, 2013; Baeza-Carratalá et al., 2016a, b). Accordingly, representatives of *Calyptoria* were fully integrated with the previous stable populations inhabiting the peri-Iberian seas.

When the extinction event took place, as a consequence of several environmental factors, a renewal of the fauna was noticed for the terebratulides and rhynchonellides (García Joral and Goy, 2000, García Joral et al., 2011) but *Calyptoria* became extinct in this event, as their spiriferinide counterparts did since the spire-bearing brachiopods failed to adapt to this super-warming event, resulting their passive feeding system crucial for their extinction in this severe biotic crisis (Ager, 1987; Vörös et al., 2016).

7. Conclusions

Taxonomical reassessment on the basis of morphometrical analyses and the examination of the internal structure of spiriferinide representatives of the genus *Calyptoria* allows updating and rearranging this genus in four species: *C. extensa* Cooper, 1989; *C. madagascariensis* (Thévenin, 1908); *C. obesa* (Cooper, 1989), and *C. vulgata* (Cooper, 1989). This updating suggests a new systematic scheme for the former attributions and emendation of the diagnosis of the genus, which is characterized externally by a conspicuous median dorsal folding pattern and obscurely ribbed flanks; this genus internally reveals a long dorsal median septum, hinge plates clearly tilted towards the dorsal valve, and spiralium arms subparallell to commissural plane.

This reassessment upholds the lower Toarcian occurrences of *L. undulata* from westernmost Tethyan areas as belonging to *Calyptoria*, thus revealing the dispersal of this Arab-Madagascan fauna from Madagascar and the Northern peri-Gondwana seas to the Western Tethys epicontinental platforms system in the Tenuicostatum Chronozone, Semicelatum Subchronozone. Accordingly, the type of *L. undulata* (Seguenza, 1885) is considered as belonging to a different evolutionary lineage. The Iberian representatives of this stock traditionally assigned to *L. undulata* are now attributed to *C. vulgata*.

ACCEPTED MANUSCRIPT

By tracking the *Calyptoria* stock records, it is possible to restrict its stratigraphical range to the uppermost Tenuicostatum Zone-lowermost Serpentinum Zone, just prior to becoming extinct with the rest of spire-bearing brachiopods.

A dispersal pathway is proposed from their Arab-Madagascan homeland along the North-Gondwana epicontinental platforms into the peri-Iberian platform system, and *C. madagascariensis* is regarded as the ancestral stock of this lineage. This group became diversified in the Arabian equatorial platform, and only *C. vulgata* spread to the West in concurrence with the thermal maximum recorded prior to the ETMEE. Thus, *Calyptoria* shows a latitudinal-controlled distribution between 0º and 30º on both hemispheres.

Dispersal of *Calyptoria* was conditioned by the interplay of several factors, emphasizing the seawater temperature and the brief larval stage (like extant rhynchonelliform brachiopods), while the contemporaneous Madagascan *Bouleiceras* ammonites were distributed in the same latitudinal range, probably also in relation with high seawater temperature, but reaching more distant areas because of their higher dispersal ability, either in life or as post-mortem drifting shells.

C. vulgata was integrated together with diverse stable assemblages well-established in the Iberian basins. Whereas the native taxa show different adaptive strategies to adapt to the environmental changes related with the extinction (e.g. size changes, stepped-extinction, endemic speciation), the response of *C. vulgata* consisted of a sudden and long spreading without outstanding morphological changes.

Similar adaptive strategies were linked to other mass extinctions such as the late Ordovician event, supporting a possible standard pattern in the response of certain brachiopod populations to such biotic crises and shedding light on the ecological effects of mass extinction events.

8. Acknowledgments

ACCEPTED MANUSCRIPT

This research is a contribution to the IGCP-655 Toarcian Oceanic Anoxic Event: Impact on marine carbon cycle and ecosystems, and was also supported by projects CGL2015-66604-R (MINECO, Government of Spain), and the Research Group VIGROB-167 (University of Alicante). We gratefully thank the Editor as well as D.A. Ruban and the other anonymous reviewer for their insightful comments and suggestions. We also appreciate M.O. Manceñido valuable advices, improvements, and enthusiastic help with literature.

9. References

Aberhan, M., 2001. Bivalve palaeobiogeography and the Hispanic Corridor: time of opening and effectiveness of a proto-Atlantic seaway. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 375–394.

Ager, D.V., 1986. Migrating fossils, moving plates and an expanding Earth. Modern Geology 10, 377–390.

Ager, D.V., 1987. Why the Rhynchonellid Brachiopods survived and the Spiriferids did not: a suggestion. Palaeontology 30(4), 853–857.

Ager, D.V., Sun, D.L., 1989: Distribution of Mesozoic brachiopods on the northern and southern shores of Tethys. Palaeontologia Cathayana 4, 23–51.

Ager, D.V., Walley, C.D., 1977. Mesozoic brachiopod migrations and the opening of the North Atlantic. Palaeogeography, Palaeoclimatology, Palaeoecology 21, 85–99.

Almerás, Y., 1987. Les Brachiopodes du Lias-Dogger: Paléontologie et Biostratigraphie. Geobios (M.S.9), 161–219.

Alméras, Y., Fauré, P., 2000. Les Brachiopodes liasiques des Pyrénées. Paléontologie, Biostratigraphie, Paléobiogéographie et Paléoenvironnements. Strata 36, 1–395.

Alméras, Y., Mouty, N., 2001: Les Brachiopodes du Jurassique de Syrie. Revue de Paléobiologie 20, 9–17.

Alméras Y., Cougnon, R., Énay, R., Mangold, C., 2010. Brachiopodes du Jurassique Inférieur et Moyen d'Arabie Saoudite Centrale. Paléontologie, Biostratigraphie et Paléoenvironnements, échelles chronostratigraphiques. Documents des Laboratoires de Géologie Lyon 168, 1–247.

Andrade, B., Duarte, L.V., García Joral, F., Goy, A., Henriques, M.H., 2016. Palaeobiogeographic patterns of the brachiopod assemblages of the Iberian Subplate during the Late Toarcian-Early Aalenian (Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 442, 12–22.

Arias C.F., Comas-Rengifo, M.J., Goy. A., Herrero, C., Ruget, C., 1992. Variations dans les associations de brachiopodes, foraminifères et ostracodes du Toarcien basal dans un secteur central de la Cordillère Ibérique. Un exemple dans la Rambla del Salto (Teruel, Espagne). Cahiers de l'Université Catholique Lyon (Sci.) 5, 5–25.

ACCEPTED MANUSCRIPT

Arkell, W.J., 1956. Jurassic Geology of the world. Oliver and Boyd, London.

Baeza-Carratalá, J.F., 2008. Patrimonio paleontológico en la colección Jiménez de Cisneros y su aplicación al estudio de los braquiópodos del Jurásico Inferior en la Cordillera Bética Oriental (provincias Alicante y Norte de Murcia). Unpublished PhD Thesis. Universidad Alicante, 906 pp.

Baeza-Carratalá, J.F., 2013. Diversity patterns of Early Jurassic brachiopod assemblages from the westernmost Tethys (Eastern Subbetic). Palaeogeography, Palaeoclimatology, Palaeoecology 381-382, 76–91.

Baeza-Carratalá, J.F. García Joral, F., 2012, Multicostate zeillerids (Brachiopoda, Terebratulida) from the Lower Jurassic of the Eastern Subbetic (SE Spain) and their use in correlation and paleobiogeography. Geologica Acta 10(3), 1–12.

Baeza-Carratalá, J.F., Sepehriannasab, B., 2014. Early Jurassic (latest Toarcian) brachiopods from the northeastern margin of the Western Tethys (Central Iran) and their paleobiogeographical significance. Geobios 47, 3–17.

Baeza-Carratalá, J.F., García Joral, F., Giannetti, A., Tent-Manclús, J.E., 2015. Evolution of the last koninckinids (Athyridida, Koninckinidae), a precursor signal of the Early Toarcian mass extinction event in the Western Tethys. Palaeogeography, Palaeoclimatology, Palaeoecology 429, 41–56.

Baeza-Carratalá, J.F., García Joral, F., Tent-Manclús, J.E., 2016a. Lower Jurassic brachiopods from the Ibero-Levantine Sector (Iberian Range): Faunal turnovers and critical bioevents. Journal of Iberian Geology 42(3), 355–369.

Baeza-Carratalá, J.F., García Joral, F., Tent-Manclús, J.E., 2016b. Brachiopod faunal exchange through an epioceanic-epicontinental transitional area from the Early Jurassic South Iberian platform system. Geobios, 49(4), 243–255.

Baeza-Carratalá, J.F., Manceñido, M.O., García Joral, F., 2016c. *Cisnerospira* (Brachiopoda, Spiriferinida), an atypical Early Jurassic spire bearer from the Subbetic Zone (SE Spain) and its significance. Journal of Paleontology 90(6), 1081–1099.

Baeza-Carratalá, J.F., Reolid, M., García Joral, F., 2017. New deep-water brachiopod resilient assemblage from the South-Iberian Palaeomargin (Western Tethys) and its significance for the brachiopod adaptive strategies around the Early Toarcian Mass Extinction Event. Bulletin of Geosciences 92(2), 233–256.

Bardin, J., Rouget, I., Benzaggagh, M., Fürsich, F.T., Cecca, F., 2015. Lower Toarcian (Jurassic) ammonites of the South Riffian ridges (Morocco): Systematics and biostratigraphy. Journal of Systematic Palaeontology 13(6), 471–501.

Behmel, H., Geyer, O.F., 1966. Beiträge zur Stratigraphie und Paläontologie des Juras von Ostspanien. III. Stratigraphie und Fossilführung im Unterjura von Albarracín (Provinz Teruel). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 124, 1–52.

Bizon, G., Champetier, Y., Guérin-Franiatte, S., Rollet, A., 1966. Présence de *Bouleiceras nitescens* dans l'est des Cordillères bétiques. Bulletin de la Société Géologique de France 8, 901–904.

ACCEPTED MANUSCRIPT

Bjerrum, C.J., Surlyk, F., Callomon, J.H., Slingerland, R.L., 2001. Numerical paleoceanographic study of the Early Jurassic Transcontinental Laurasian Seaway. Paleoceanography 16, 390–404.

Blaison, J., 1968. Affinités, répartition et typologie du genre *Bouleiceras* Thévenin, 1906. Annales scientifiques de l'université de Besançon 5, 41–49.

Callomon, J.H., 1979. Marine boreal Bathonian fossils from the northern North Sea and their palaeogeographical significance. Proc. Geol. Assoc. Lond. 90, 163–169.

Calzada, S., 1981. Niveles de braquiópodos del Lías de Camarasa (Lérida). Cuadernos de Geología Universidad de Granada 10, 197–211.

Cecca, F., Macchioni, F., 2004. The two Early Toarcian (Early Jurassic) extinction events in ammonoids. Lethaia 37, 35–56.

Champetier, Y., 1972. Le Prébétique et Ibérique côtiers dans le Sud de la Province de Valence et le Nord de la Province d'Alicante (Espagne). Nancy (Thèse Doct.) Sciences de la Terre. Mémoire 24, 170 pp.

Chiocchini, M., Fazzuoli, M., Pavia, G. 2002: The Uanei Formation (Toarcian) in the Iscia Baidoa Area, South Western Somalia. In: L. Martire (ed.), 6th International Symposium on the Jurassic System. Abstracts and Program, 33–34. Mondello.

Colás, J., 2008. Las sucesiones de braquiópodos del Toarciense inferior en Calanda (provincia de Teruel, España). Geotemas 10, 1257–1260.

Colmenar, J., 2015. The arrival of brachiopods of the *Nicolella* Community to the Mediterranean margin of Gondwana during the Late Ordovician: Palaeogeographical and palaeoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 428, 12–20.

Comas-Rengifo, M.J., 1982. El Pliensbachiense de la Cordillera Ibérica. Unpublished PhD. Universidad Complutense de Madrid, 591 pp., 18 pl.

Comas-Rengifo, M.J., Goy, A., 1975. Estratigrafía y paleontología del Jurásico de Ribarredonda (Guadalajara). Estudios Geológicos 31, 297–339.

Comas-Rengifo, M.J., Gomez, J.J., Goy, A, Arias, C., Bernad, J., García Joral, F., Herrero, C., Martínez, G., Perilli, N., 1996. The Toarcian in the Rambla del SaIto (Sierra Palomera) Section. 15th Toarcian and 4th Aalenian Working Groups Meeting. Fieldtrip Iberian Range Guide-Book (Department of Paleontology. Universidad Complutense de Madrid), 27–48.

Comas-Rengifo, M.J., García Joral, F., Goy, A., 2006. Spiriferinida (Brachiopoda) del Jurásico Inferior del NE y N de España: distribución y extinción durante el evento anóxico oceánico del Toarciense Inferior. Boletín Real Sociedad Española de Historia Natural, Sec. Geológica 101, 147–157.

Comas-Rengifo, M.J., Duarte, L.V., García Joral, F., Goy, A., 2013. Los braquiópodos del Toarciense Inferior (Jurásico) en el área de Rabaçal-Condeixa (Portugal): distribución estratigráfica y paleobiogeografía. Comunicações Geológicas 100(1), 37–42.

Comas-Rengifo, M.J., Duarte, L.V., Félix, F.F., García Joral, F., Goy, A., Rocha, R.B., 2015. Latest Pliensbachian–Early Toarcian brachiopod assemblages from the Peniche section (Portugal) and their

ACCEPTED MANUSCRIPT

correlation. Episodes 38(1), 2–8.Cooper, G.A., 1989. Jurassic Brachiopods of Saudi Arabia. Smithsonian Contributions to Paleobiology 65, 1–213.

Damborenea, S.E., 2000. Hispanic Corridor: its evolution and the biogeography of bivalve molluscs. In: Hall, R.L. and Smith, P.L. (Eds.): Advances in Jurassic Research. Proceedings of the Fifth International Symposium on the Jurassic System, Georesearch Forum 6, 369–380.

Damborenea, S.E. 2002. Jurassic evolution of Southern Hemisphere marine palaeobiogeographic units based on benthonic bivalves. Geobios M.S. 24, 51–77.

Delance, J.H., 1969. Étude de quelques Brachiopodes liasiques du Nord-Est de l'Espagne. Annales de Paléontologie, (Invertébrés) 55(1), 1–44.

Dera, G., Neige, P., Dommergues, J.L., Brayard, A., 2011. Ammonite paleobiogeography during the Pliensbachian–Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Global and Planetary Change 78, 92–105.

Dommergues, J.L., Meister, C., Mouterde, R., 1997. Pliensbachien. Bioestratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossils. In: Cariou, E. and Hantzpergue, P. (Eds.). Bull. Centre Rech. Elf Explor. Prod., Pau 17, 15–24.

Dubar, G., Mouterde, R., 1953. Découverte d'ammonites à affinités arabomalgache (*Bouleiceras*) dans le Toarcien inférieur du Portugal. Comptes-rendus de l'Académie des Sciences, Paris 237, 575–576.

Dubar, G., Elmi, S., Mouterde, R., 1970. Remarques sur le Toarcien d'Albarracin et sur sa faune de *Bouleiceras*. Comptes-rendus sommaires de la Société géologique de France 5, 162–163.

Elmi, S., Rulleau, L., Gabilly, J., Mouterde, R., 1997. Toarcien. Bioestratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossils. In: Cariou, E. and Hantzpergue, P. (Eds.). Bull. Centre Rech. Elf Explor. Prod., Pau 17, 25–36.

El-Sorogy, A.S., Gameil, M., Youssef, M., Al-Kahtany, K.M., 2017. Stratigraphy and macrofauna of the Lower Jurassic (Toarcian) Marrat Formation, central Saudi Arabia. Journal of African Earth Sciences 134, 476–492.

Enay, R., Mangold, C., 1994. Première zonation par ammonites du Jurassique d'Arabie Saoudite, une référence pour la province arabique. In: Cariou, E., Hantzpergue, P. (Eds.), 3e Symposium International de Stratigraphie du Jurassique, Poitiers, 2e édition. Geobios (MS 17), 161–174.

Fernández López, S., García Joral, F., Gómez, J.J., Henriques, M.H., Martínez, G., 1998. La diferenciación paleogeográfica de la Cuenca Catalana al principio del Jurásico Medio. Revista Española de Paleontología 11 (1-2), 3–22.

Ferrari, S., Damborenea, S., Manceñido, M., Griffin, M., 2015. Early Jurassic Trochotomidae (Vetigastropoda, Pleurotomarioidea) from the Neuquén Basin, Argentina. Journal of Paleontology 89(2), 331–345.

García Joral F., Goy, A., 2000. Stratigraphic distribution of Toarcian brachiopods from the Iberian Range and its relation to depositional sequences. Georesearch Forum 6, 381–386.

ACCEPTED MANUSCRIPT

García Joral, F., Gómez, J.J., Goy, A., 2011. Mass extinction and recovery of the Early Toarcian (Early Jurassic) brachiopods linked to climate change in northern and central Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 302, 367–380.

García Joral, F., Baeza-Carratalá, J.F., Goy, A., 2015. Size changes in brachiopods associated to the Early Toarcian (Jurassic) Mass Extinction Event. In: Huang, B., Shen, S. (Eds.): The Brachiopod World. Abstracts for IBC 7. Permophiles 61 (1), 30–31.Geiger, M. ; Clark, D. N. ; Mette, W. 2004. Reappraisal of the timing of the breakup of Gondwana based on sedimentological and seismic evidence from the Morondava Basin, Madagascar. Journal of African Earth Sciences 38, 363–381.

Geiger, M., Schweigert, G., 2006. Toarcian-Kimmeridgian depositional cycles of the south-western Morondava Basin along the rifted continental margin of Madagascar. Facies 52, 85–112.

Geyer, O.F., 1965. Einige funde der arabomadagassischen Ammonitengattung *Bouleiceras* im Unterjura der Iberischen Halbinsel. Paläontologische Zeitschrift 39 (1–2), 26–32.

Geyer, O.F., 1971. Sur l'âge du niveau à *Bouleiceras* dans le Lias d'Albarracin. Comptes Rendus sommaires des séances de la Société géologique de France 6, 319–320.

Gómez, J.J., Goy, A., 2000. Definition and organization of limestone-marl cycles in the Toarcian of the Northern and East-Central part of the Iberian Subplate (Spain). GeoResearch Forum 6, 301–310.

Gómez, J.J., Goy, A., 2005. Late Triassic and Early Jurassic palaeogeographic evolution and depositional cycles of the Western Tethys Iberian platform system (Eastern Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 222, 77–94.

Gómez, J.J., Goy, A., 2011. Warming-driven mass extinction in the Early Toarcian (Early Jurassic) of northern and central Spain. Correlation with other time-equivalent European sections. Palaeogeography, Palaeoclimatology, Palaeoecology 306, 176–195.

Gómez, J.J., Comas-Rengifo, M.J., Goy, A., 2016. Palaeoclimatic oscillations in the Pliensbachian (Early Jurassic) of the Asturian Basin (Northern Spain). Climate of the Past 12, 1199–1214.

Goy, A., 1974. El Lías de la mitad norte de la rama castellana de la Cordillera Ibérica. Unpublished PhD. Universidad Complutense de Madrid, 940 pp.

Goy, A., 1975. Nuevos hallazgos de faunas arabomalgaches del Toarciano inferior en la Cordillera Ibérica. Coloquios de Paleontología, 28, 3–9.

Goy, A., Comas-Rengifo, M.J., Arias, C., García Joral, F., Gómez, J.J., Herrero, C., Martínez, G., Rodrigo, A., 1997. El Tránsito Pliensbachiense/Toarciense en el sector central de la Rama Aragonesa de la Cordillera Ibérica (España). Cahiers de l'Université Catholique de Lyon 10, 159–179.

Goy, A., Comas-Rengifo, M.J., García Joral, F., 1984. The Liassic Brachiopods of the Iberian Range (Spain): Stratigraphic Distribution and Biozonation. In: O. Michelsen, A. Zeiss (eds.), International Symposium on Jurassic Stratigraphy. Symposium vol. I., 227–250.

Goy, A., Martínez, G., 1996. Distribución bioestratigráfica de los Bouleiceratinae en las Cuencas Ibérica y Vasco-Cantábrica. Tomo extraordinario, 125 Aniv. Real Sociedad Española de Historia Natural, 306–310.

ACCEPTED MANUSCRIPT

Goy, A., Martínez, G., Rivas, P., 1988. Difficulties in correlating the Toarcian ammonite succession of the Iberian and Betic Cordilleras. In: Rocha, R., Soares, A.F. (Eds.), 2nd International Symposium on Jurassic Stratigraphy, Lisboa, 155–178.

Guex, J. (1974). Les Bouleaceratinae Arkell (Ammonitina, Cephalopoda): sous-famille mono- ou polyphylétique? Eclogae Geologicae Helvetiae, Bâle 67 (2), 427-430.

Hallam, A., 2001. A review of the broad pattern of Jurassic sea-level changes and their possible causes in the light of current knowledge. Palaeogeography, Palaeoclimatology, Palaeoecology 167 (1-2), 23–37.

Hammer, Ø. and Harper, D.A.T., 2006: Paleontological data analysis, 351 pp. Blackwell Publishing, Oxford.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4, 1–9.

He, W., Zhang, K., Chen, Z.Q., Yan, J., Yang, T., Zhang, Y., Gu, S., Wu, S., 2015. A new genus *Liaous* of early Anisian Stage (Middle Triassic) brachiopods from southwestern China: systematics, reassessment of classification of the Spiriferinioidea, community paleoecology, and paleoenvironmental implications. Journal of Paleontology 89(6), 966–979.

Herrero, C., 1993. Los foraminíferos del Toarciense inferior de la Cordillera Ibérica. Colección Tesis Doctorales UCM 87, 1–524

Hillebrandt, A. v., 1973. Die ammonitengattungen *Bouleiceras* und *Frechiella* im Jura von Chile und Argentinien. Eclogae Geologicae Helvetiae 66(2), 351–363.

Hillebrandt, A. v., 1984. The faunal relations of the Lower Jurassic ammonites of South America. In: Michelsen, O., Zeiss, A. (Eds.), International symposium on Jurassic stratigraphy, Erlangen, 715–729.

Hillebrandt, A. v., 1987. Liassic ammonite zones of South America and correlations with others provinces. In: Volkheimer, W. (Ed.), Bioestratigrafía de los Sistemas Regionales del Jurásico y Cretácico en América del Sur, Mendoza, 111–157.

Hillebrandt, A. v., 2006. Ammoniten aus dem Pliensbachium (Carixium und Domerium) von Sudamerika. Revue de Paléobiologie 25(1): 1–403.

Hillebrandt, A., v., Schmidt-Effing, R., 1981. Ammoniten aus dem Toarcium von Chile. Zitteliana 6, 3–74.

Korte, C., Hesselbo, S.P., Ullmann, C.V., Dietl, G., Ruhl, M., Schweigert, G., Thibault, N., 2015. Jurassic climate mode governed by ocean gateway. Nature Communications 6:10015, doi: 10.1038/ncomms10015.

Macchioni, F., Cecca, F., 2002. Biodiversity and biogeography of middle–late liassic ammonoids: implications for the Early Toarcian mass extinction. Geobios (M.S.24), 165–175.

Manceñido, M.O., 1981, A revision of Early Jurassic Spiriferinidae (Brachiopoda, Spiriferida) from Argentina: Cuencas Sedimentarias del Jurásico y Cretácico de América del Sur 2, 625–660.

Manceñido, M.O., 1990. The succession of Early Jurassic brachiopod faunas from Argentina: correlation and affinities. In: MacKinnon, D.I., Lee, D.E., Campbell, J.D. (Eds.), Brachiopods through Time, Proceedings Second International Brachiopod Congress. A.A. Balkema, Rotterdam, 397–404.

ACCEPTED MANUSCRIPT

Manceñido, M.O., 1993. Early Jurassic Brachiopods from Greece: a review. In: Pálfy, J., Vörös, A. (Eds.), Mesozoic Brachiopods of Alpine Europe. Hungarian Geological Society, pp. 79–100.

Manceñido, M.O., 2002. Paleobiogeography of Mesozoic brachiopod faunas from Andean–Patagonian areas in a global context. Geobios 35, (M.S. 24), 176–192.

Manceñido, M.O., 2004. Las "espiriferinas" del Jurásico Inferior: Una mirada retrospectiva a los estudios de Daniel Jiménez de Cisneros. Geo-Temas 7, 269–272.

Manceñido, M.O., Dagys, A.F., 1992. Brachiopods of the circum-Pacific region. In: Westermann, G.E.G. (Ed.): The Jurassic of the Circum-Pacific. World and Regional Geology, 3. Cambridge University Press, 328–333.

Mouterde, R., 1953. Une forme d'affinites Arabo-Malgaches, *Bouleiceras* dans le Toarcien Inferieur de Coimbra. Boletim da Sociedade Geológica de Portugal 11 (1), 93–99.

Mouterde, R., 1970. Age toarcien et répartition du genre *Bouleiceras* dans la péninsule ibérique. Comptes-rendus sommaires des séances de la Société géologique de France 5, 163–164.

Mouterde, R., 1971. Une coupe du Lias à Obon aux confins des provinces de Teruel et de Saragosse. Cuadernos de Geología Ibérica 2, 345–354.

Mouterde, R., Rocha, R., 1981. Le Lias de la région de Rio de Couros (Portugal). Boletim da Sociedade Geológica de Portugal 22, 209–220.

Page, K.N., 2003. The Lower Jurassic of Europe: its subdivision and correlation. Geological Survey Denmark and Greenland Bulletin 1, 23–59.

Poulton, T.P., Callomon, J.H., 1977. A new species of trigoniid bivalve from the Boreal Bathonian (Jurassic) of central East Greenland. Bull. Geol. Soc. Denmark 26, 155–159.

Pozza, G.C. 2001. An answer to the proposal of synonymy *Spiriferina* D'Orbigny, 1847 (=*Liospiriferina* Rousselle, 1977) and *Calyptoria* Cooper, 1989 (=*Cingolospiriferina* Pozza, 1992) in J.L. Carter et al., 1994. Revue de Paléobiologie 20(1), pp.1–7.

Riccardi, A.C., Damborenea, S.E., Manceñido, M.O., Leanza, H.A., 2011. Megainvertebrados del Jurásico y su importancia geobiológica. Relatorio del XVIII Congreso Geológico Argentino, Neuquén, 2011 441–464.

Rousselle, L., 1977. Spiriférines du Lias moyen et supérieur au Maroc (Rides prérifaines, Moyen Atlas) et en Espagne. Notes et Mémoires du Service Géologique du Maroc 38, 153–175.

Rulleau, L., Bécaud M., Neige, P., 2003. Les ammonites traditionnellement regroupées dans la sous-famille des Bouleiceratinae (Hildoceratidae, Toarcien): aspects phylogénétiques, biogéographiques et systématiques. Geobios 36, 317–348.

Seguenza, G., 1885. Monografia delle Spiriferina dei varii piani del Lias Messinese: Bollettino della Società Geologica Italiana 4, 377–497.

Sha, J., 2002. Hispanic Corridor formed as early as Hettangian: on the basis of bivalve fossils. Chin. Sci. Bull. 47, 414–417.

ACCEPTED MANUSCRIPT

Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchérasmarx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F. 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. Earth andPlanetary Science Letters 290, 448–458.

Thévenin, A., 1908. Paléontologie de Madagascar, 5: fossiles liasiques. Annales de Paléontologie 3 (3), 1–39.

Vörös, A., 2002. Victims of the Early Toarcian anoxic event: the radiation and extinction of Jurassic Koninckinidae (Brachiopoda). Lethaia 35, 345–357.

Vörös, A., 2005. The smooth brachiopods of the Mediterranean Jurassic: refugees or invaders? Palaeogeography, Palaeoclimatology, Palaeoecology 223, 222–242.

Vörös, A., 2009. The Pliensbachian brachiopods of the Bakony Mountains (Hungary): Geologica Hungarica, series Paleontologica, 58, 1–300.

Vörös, A., 2016. Early Jurassic (Pliensbachian) brachiopod biogeography in the western Tethys: the Euro-Boreal and Mediterranean faunal provinces revised. Palaeogeography, Palaeoclimatology, Palaeoecology 457, 170–185.

Vörös, A., Kocsis, Á.T., Pálfy, J. 2016. Demise of the last two spire-bearing brachiopod orders (Spiriferinida and Athyridida) at the Toarcian (Early Jurassic) extinction event. Palaeogeography, Palaeoclimatology, Palaeoecology 457, 233–241.

Westermann, G.E.G. 2000. Marine faunal realms of the Mesozoic: review and revision under the new guidelines for biogeographic classification and nomenclature. Palaeogeography, Palaeoclimatology, Palaeoecology 163, 49–68.

Figure captions

Fig. 1. Location of the Upper Pliensbachian-Lower Toarcian studied outcrops in the peri-Iberian platforms system, emphasizing the occurrences of the *Calyptoria* stock among the brachiopod assemblages distribution. Map modified after Andrade et al. (2016). Source of the brachiopod assemblage's distribution: García Joral et al. (2011) for localities 1-2 and 5-7; Calzada (1981) for locality 3; Fernández-López et al. (1998) for loc. 4; Rousselle (1977) for loc. 8; Colás (2008) for loc. 9; Goy (1974) for locs. 10, 12; Comas-Rengifo and Goy (1975) for loc. 11; Comas-Rengifo (1982) for loc. 13; Comas-Rengifo et al. (1996) for loc. 14; Baeza-Carratalá et al. (2016a) for locs. 15-16; Baeza-Carratalá et al. (2016b) for loc. 17; Baeza-Carratalá (2013) for loc. 18; Comas-Rengifo et al. (2013) for loc. 19; Comas-Rengifo et al. (2015) for loc. 20.

ACCEPTED MANUSCRIPT

Fig. 2. Stratigraphical sections embracing all the peri-Iberian basins where *Calyptoria* stock has been recorded, showing the distribution of the brachiopod assemblages. **A-C**. Ibero-Levantine sector of the Iberian Range (A: Sot de Chera; B: Benifairó; C: Racó de Joana). **D.** Transitional external Betic Zone (La Mola section). **E.** External Subbetic Zone (Tarabillo section). **F**. Aragonese branch of the Iberian Range (Ariño section). **G**. Lusitanian basin (Fonte Coberta section). Logs based on data from Baeza-Carratalá et al., 2016a (A-C); Baeza-Carratalá et al., 2016b (D), Garcia Joral et al., 2011 (F) and Comas-Rengifo et al. 2013 (G)

Fig. 3. Main biometric parameters measured in the morphological analysis (modified after Manceñido, 1981). L: length; W: width; T: thickness; lvd: length of dorsal valve; Mw: position of maximum width in the shell-length; ha: height of cardinal area; hf: height of dorsal median fold; wf: width of dorsal median fold.

Fig. 4. Paleogeographical map of the Toarcian, modified after Damborenea (2002) and Ferrari et al. (2015), showing the paleobiogeographical distribution of the *Calyptoria* brachiopod genus indicative of an inter-tropical restricted distribution at paleolatitudes between 30°N and 30°S, preferentially inhabiting epioceanic platforms and suggesting a dispersal pathway from the peri-Gondwana paleomargin to the peri-Iberian platform system. The distribution of the associated *Bouleiceras* Ammonite Fauna is also recorded.

Fig. 5. Scatter plots of the studied specimens in the spaces defined by the two first axis of the Principal Component Analysis (PCA) applied to the *Calyptoria* representatives. **A**. Plot of all the specimens without spatial or specific differentiation. Dimensional vectors have been superimposed to the PCA values showing the main discriminating factors; the type specimen of each nominal species analyzed is represented by an asterisk and a drawing (in dorsal and anterior views) for better understanding the

ACCEPTED MANUSCRIPT

similarity relationship among them. **B.** Specimen scores clustered considering the region where they were recorded, showing a diverse occupation of the morpho-space and suggesting a biogeographical differentiation. **C**. Dataset ordination of PCA values interpreted in terms of taxonomical discrimination of the valid species recognized herein.

Fig. 6. Internal structure of *Calyptoria vulgata* (Cooper). **A**. Transverse serial sections through the specimen SC1a.23.5 from Sot de Chera section (distance from the beak in mm)**. B-F**. Microphotographs of acetate peels from the same specimen. (B). Section at 0.60 mm from the apex showing pedicle collar, ventral median septum, and dental plates dorsally convergent. (C) Section at 3.00 from the apex, showing a highly striated cardinal process and incipient hinge plates. (D) Section at 3.70 mm from the apex, showing a low dorsal median septum, hinge teeth interlocked in the sockets and dorsally oriented hinge plates. (E) Partial section at 5.80 mm from the apex, showing a spiralium arm arrangement. (F) Partial section at 9.00 mm from the apex, showing a well-developed jugum and the arrangement of successive whorls of a spiralium arm. **G.** Serially sectioned specimen SC1a.23.5 in dorsal, lateral and anterior views.

Fig. 7. Internal structure of *Calyptoria vulgata* (Cooper). **A**. Transverse serial sections through the specimen SL.5.8 from Racó de Joana section (distance from the beak in mm). **B-F**. Microphotographs of acetate peels from the same specimen. (B). Section at 1.60 mm from the apex showing pedicle collar fused to the ventral median septum and dental plates. (C, D) Sections at 2.60 and 2.80 mm from the apex, showing the first stages of hinge plates and striated ctenophoridium of cardinal process. (E) Section at 3.80 mm from the apex, showing the cardinal area and hinge plates tilted towards dorsal valve. (F) Partial section at 9.70 mm from the apex, showing a well-developed jugum. **G.** Serially sectioned specimen SL.5.8 in dorsal, lateral and anterior views.

ACCEPTED MANUSCRIPT

Fig. 8. Internal structure of *Calyptoria vulgata* (Cooper). **A**. Transverse serial sections through the specimen DB.6.10 from Benifairó section (distance from the beak in mm). **B.** Serially sectioned specimen DB.6.10 in dorsal, lateral and anterior views. **C-I**. Microphotographs of acetate peels from the same specimen. (C). Section at 1.20 mm from the apex showing apical system with dental plates, ventral median septum and pedicle collar joined, and also revealing short deltidial plates. (D) Section at 2.40 mm from the apex, showing the striated cardinal process. (E) Section at 2.50 mm from the apex, showing the ending of the cardinal process, evidencing the wide depressed cardinal platform and the hinge plates, initially attached to the dorsal valve. (F) Partial section at 3.00 mm from the apex, showing the interlocked hinge tooth and socket and the presence of denticula. (G-I) Partial sections at 5.90, 6.30, and 6.70 mm respectively from the apex revealing the spiralia progress, where a mainly subparallel development between lamellae from successive whorls of each spiralium is noticed.

Fig. 9. Intraspecific variability of *Calyptoria vulgata* (Cooper) from the peri-Iberian platforms system. All specimens (except for 12) were coated with magnesium oxide. In 1-11: (a) dorsal, (b) lateral, and (c) anterior views. **1.** Specimen TaSu.Z2.1 from the Subbetic area. **2-6**. Specimens from the Ariño section (Iberian Range): 2, Specimen 1.Ar.79.1; 3, Specimen 1.Ar.79.7; 4, Specimen 1.Ar.79.10; 5, Specimen 1.Ar.78.1; 6, Specimen 1.Ar.8.20.2. **7-10**. Representatives of the Ibero-Levantine Sector of the Iberian Range (7-9 from Racó de Joana section, 10 from Benifairó section): 7, Specimen SL.5.2; 8, Specimen SL.5.1; 9: Specimen SL.5.3; 10: Specimen DB.6.1. **11**. Specimen FC.14.21 from the Fonte Coberta section (Portugal). **12**. Specimen 1.Ar.8.202 from the Ariño section (Iberian Range) showing the arrangement of microornamentation consisting on very fine and dense spinules on the external layer of the shell (12 a: ventral view), alternating with decorticated areas as shown in the detail view (12 b).

Fig. 10. Correlation sketch showing the sudden and short temperature-driven dispersal event inferred for *Calyptoria* representatives, which mainly occurred in the Tenuicostatum Chronozone, Semicelatum

ACCEPTED MANUSCRIPT

Subchronozone (notice that the record is virtually synchronous in all the basins considered). Relative abundance in the assemblages of this community suggests its settlement restricted to the epicontinental seas, being epioceanic platforms of the Mediterranean bioprovince only a passageway between the Arab-Madagascan regions and the Euro-Boreal bioprovinces. Paleotemperature data are based on Gómez and Goy (2011), Korte et al. (2015), and Gomez et al. (2016); dashed lines indicate uncertainty in the dating.

Table 1: Eigenvalues and relative weight of the axes obtained in the performed PCA.

Table 2. Re-arrangement of the representatives of the *Calyptoria* lineage with synonymy of each species herein recognized as valid and attributed to the genus *Calyptoria*. ILS: Ibero-Levantine Sector of the Iberian Range; *(vid.):* specimen directly checked by the authors.

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

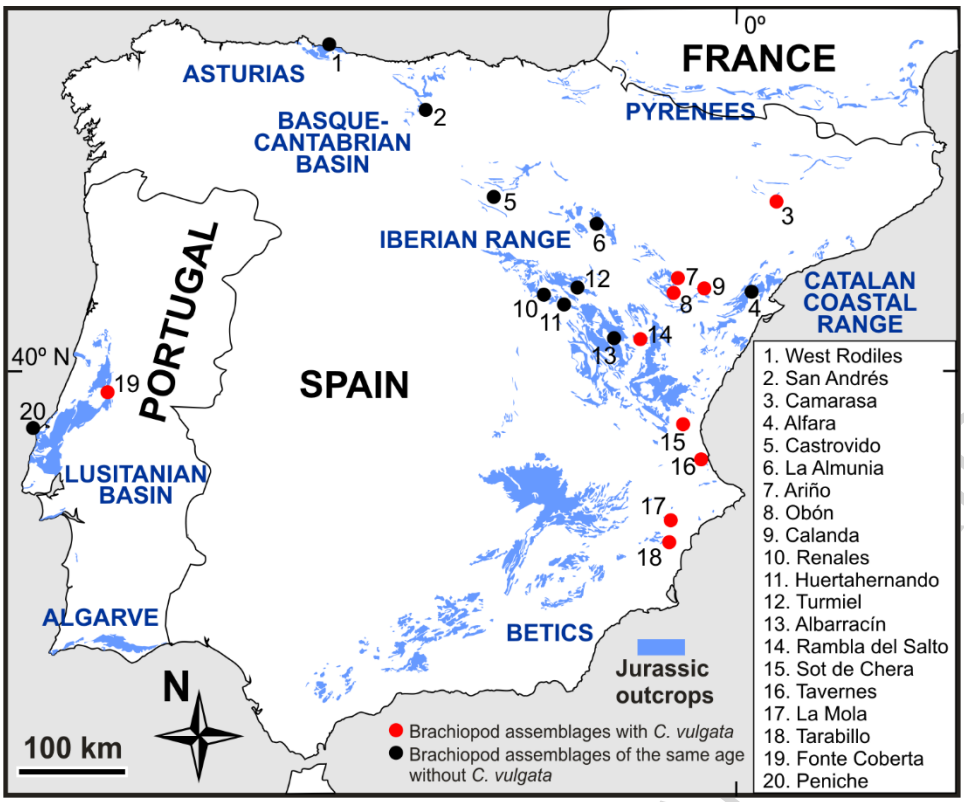


Fig. 1

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

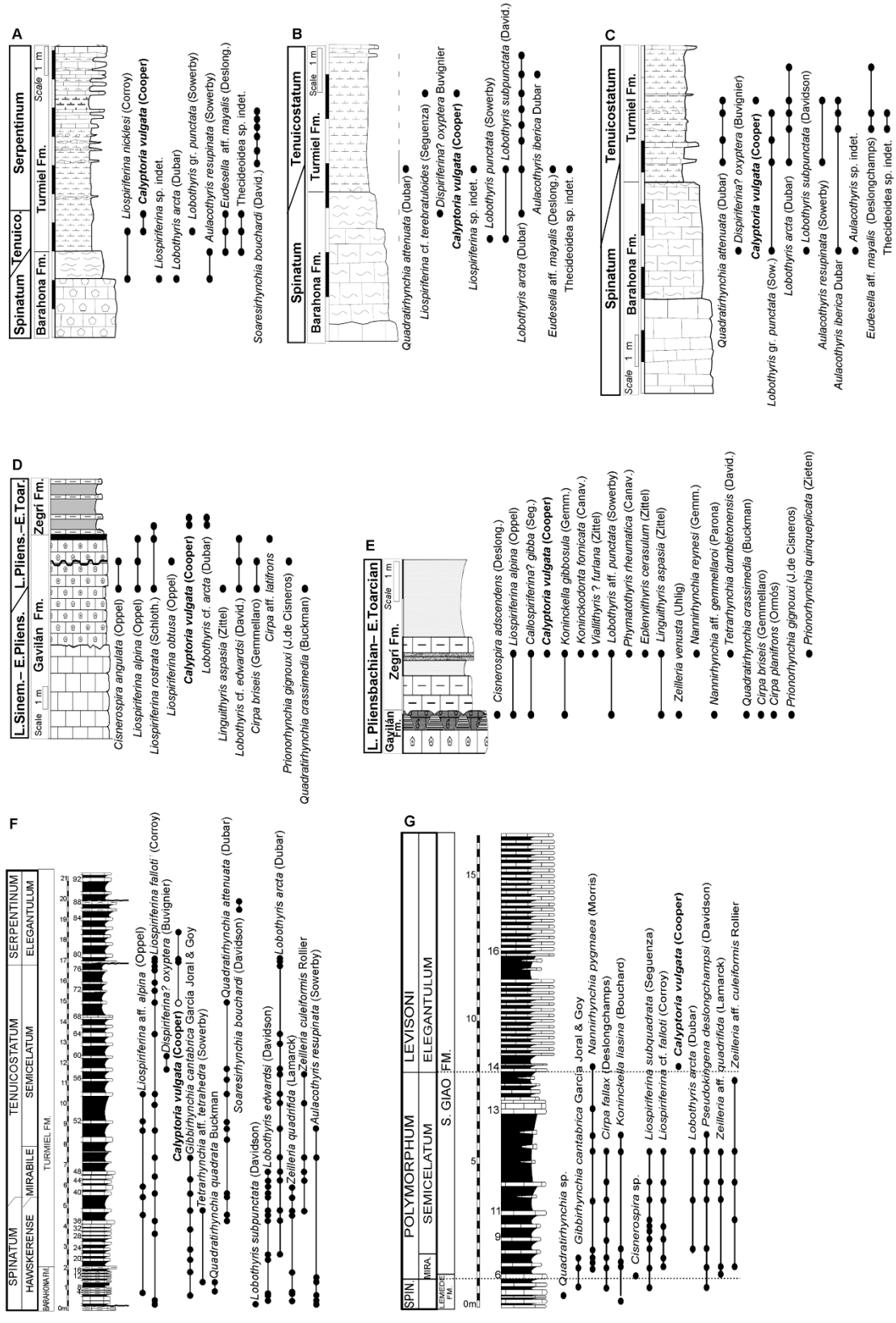


Fig.2

ACCEPTED MANUSCRIPT

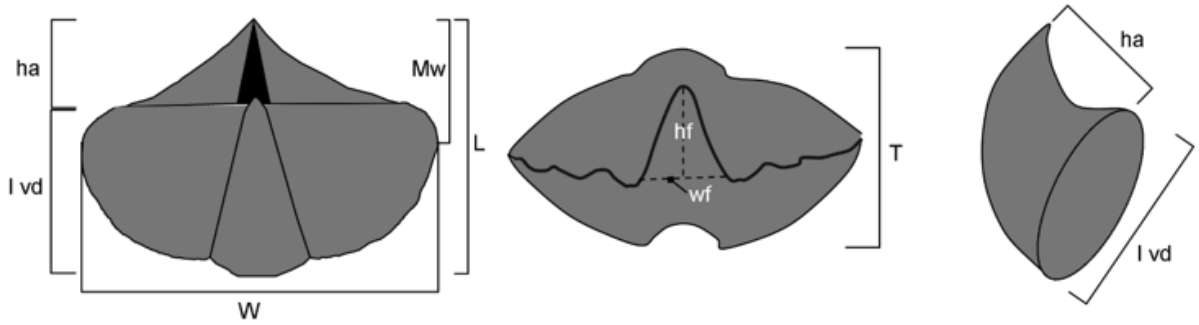


Fig. 3

ACCEPTED MANUSCRIPT

ACCEPTED MANUSCRIPT

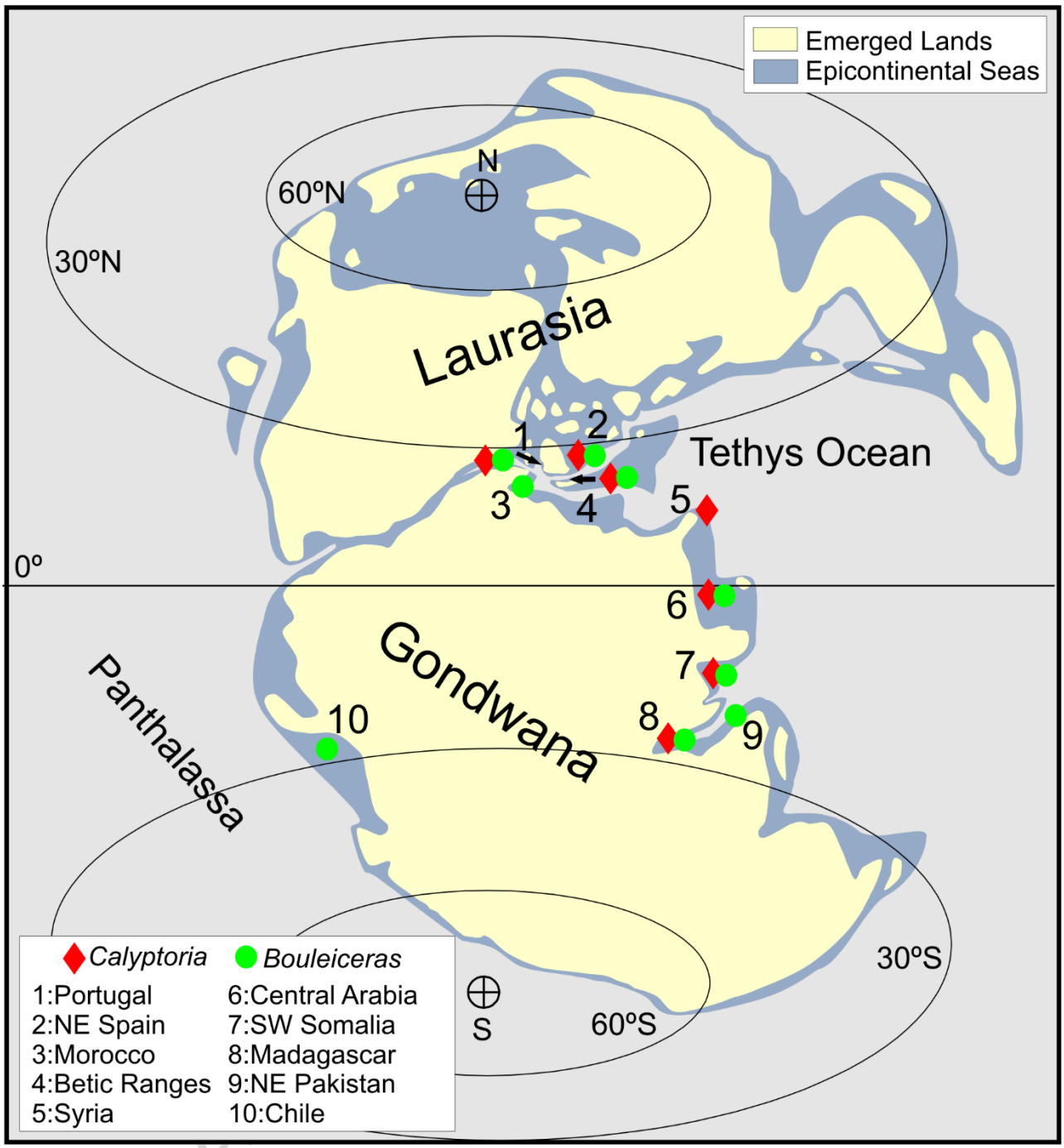


Fig. 4

ACCEPTED MANUSCRIPT

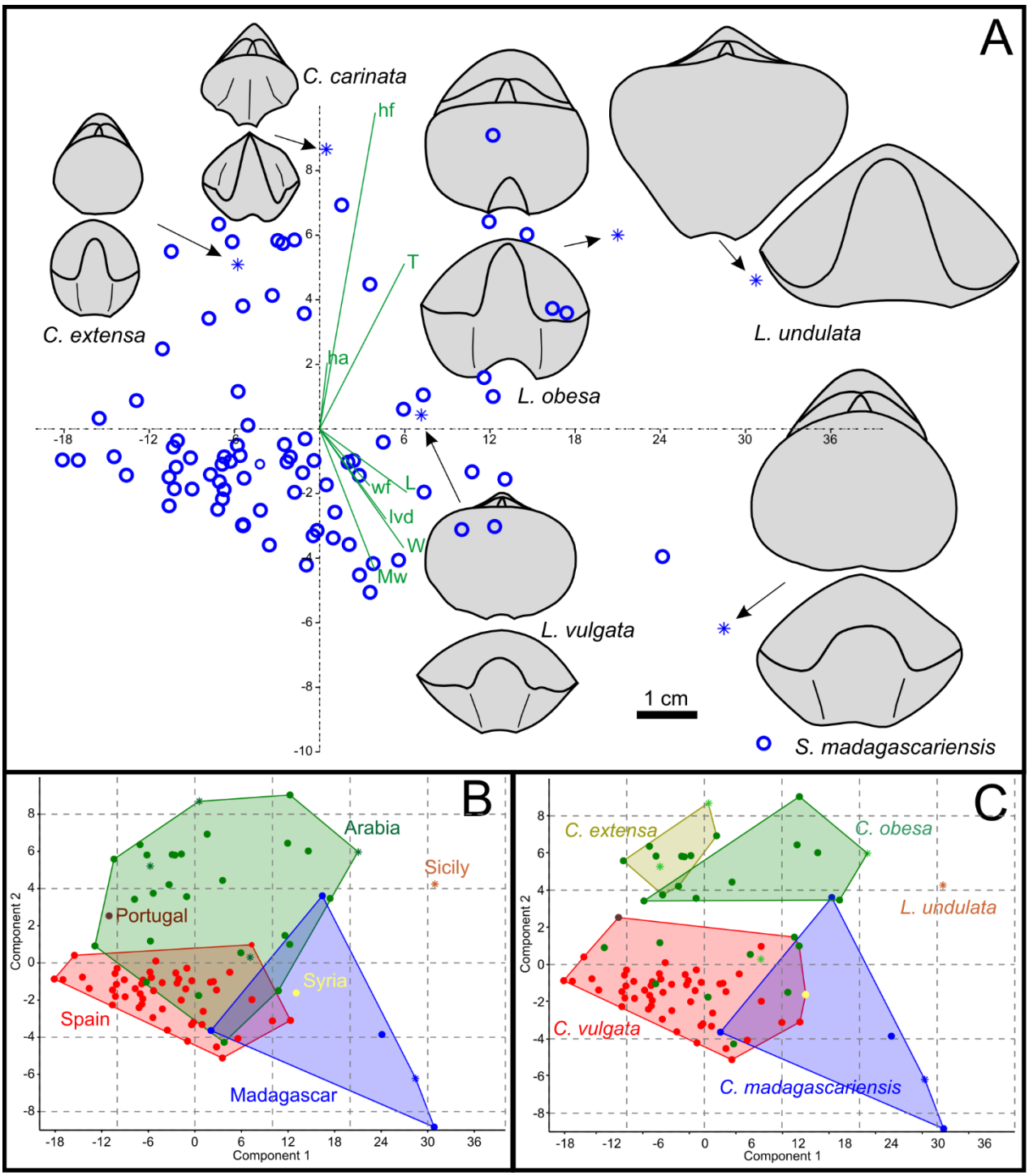


Fig. 5

ACCEPTED MANUSCRIPT

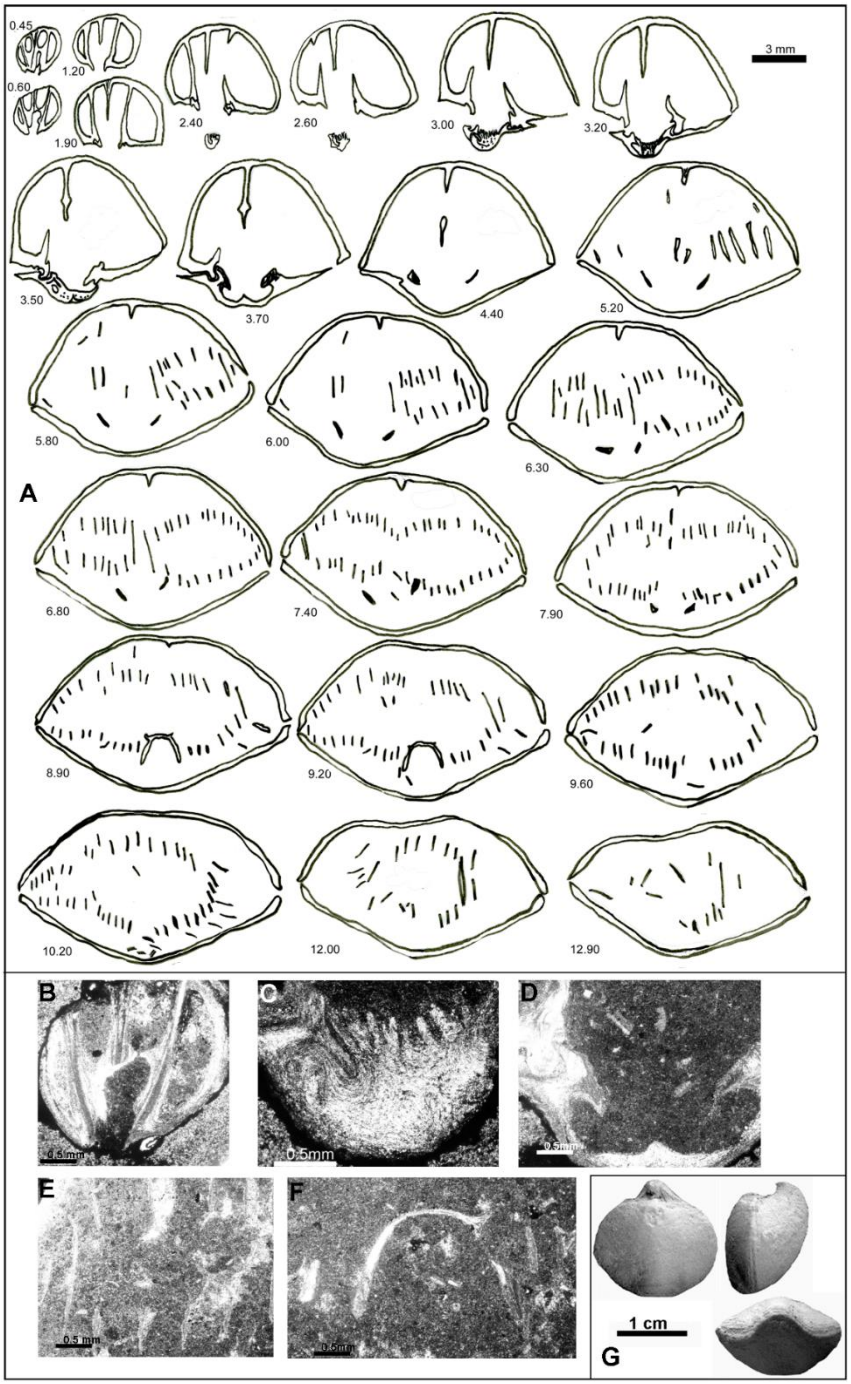


Fig. 6

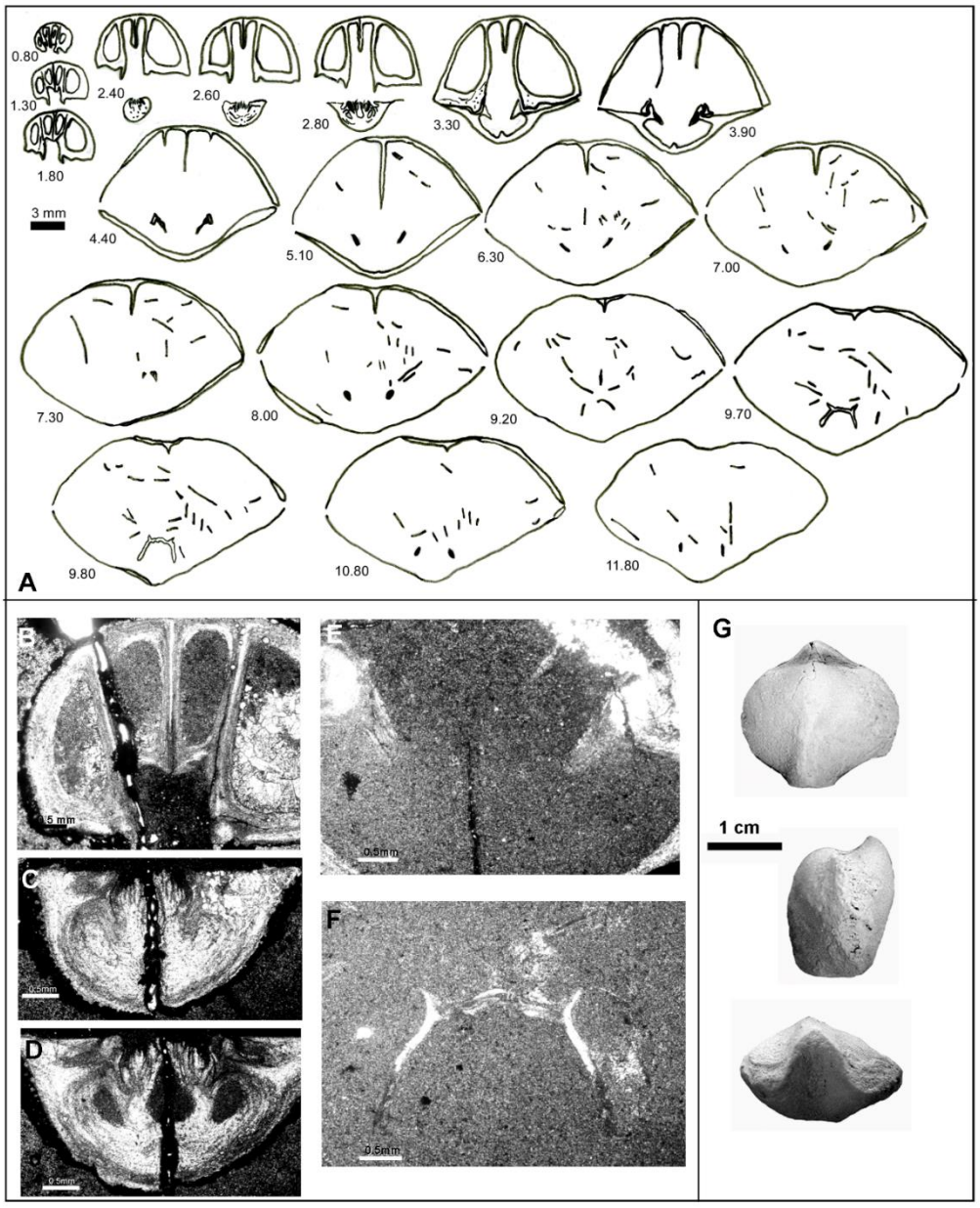

0.80
1.30
1.80
2.40
2.60
2.80
3.30
3.90
3 mm
4.40
5.10
6.30
7.00
7.30
8.00
9.20
9.70
9.80
10.80
11.80
A
B
C
D
E
F
G
1 cm

Fig. 7

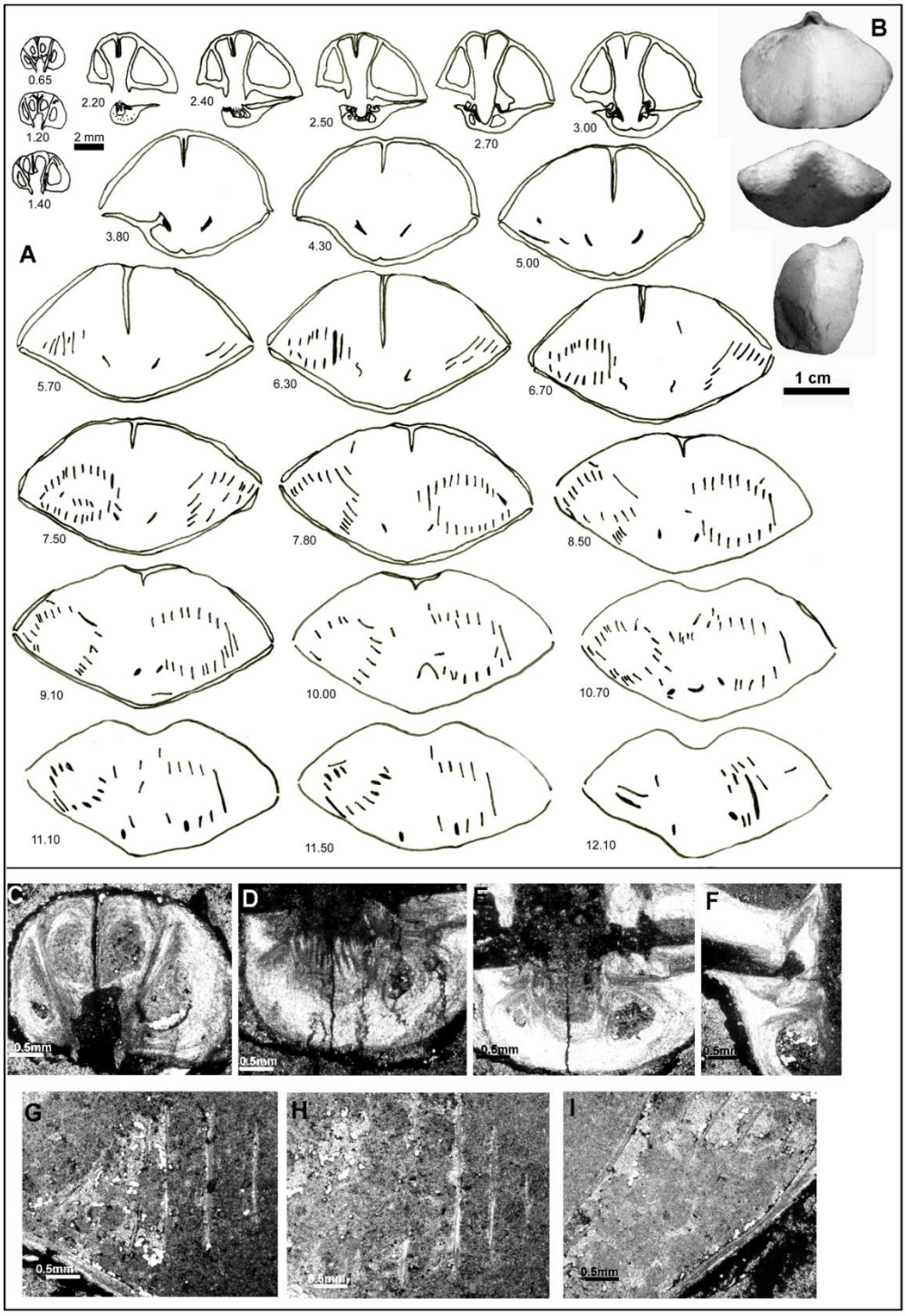

A
B
0.65
1.20
1.40
2.20
2.40
2.50
2.70
3.00
2 mm
3.80
4.30
5.00
5.70
6.30
6.70
1 cm
7.50
7.80
8.50
9.10
10.00
10.70
11.10
11.50
12.10
C
D
E
F
G
H
I
0.5mm

Fig. 8

ACCEPTED MANUSCRIPT

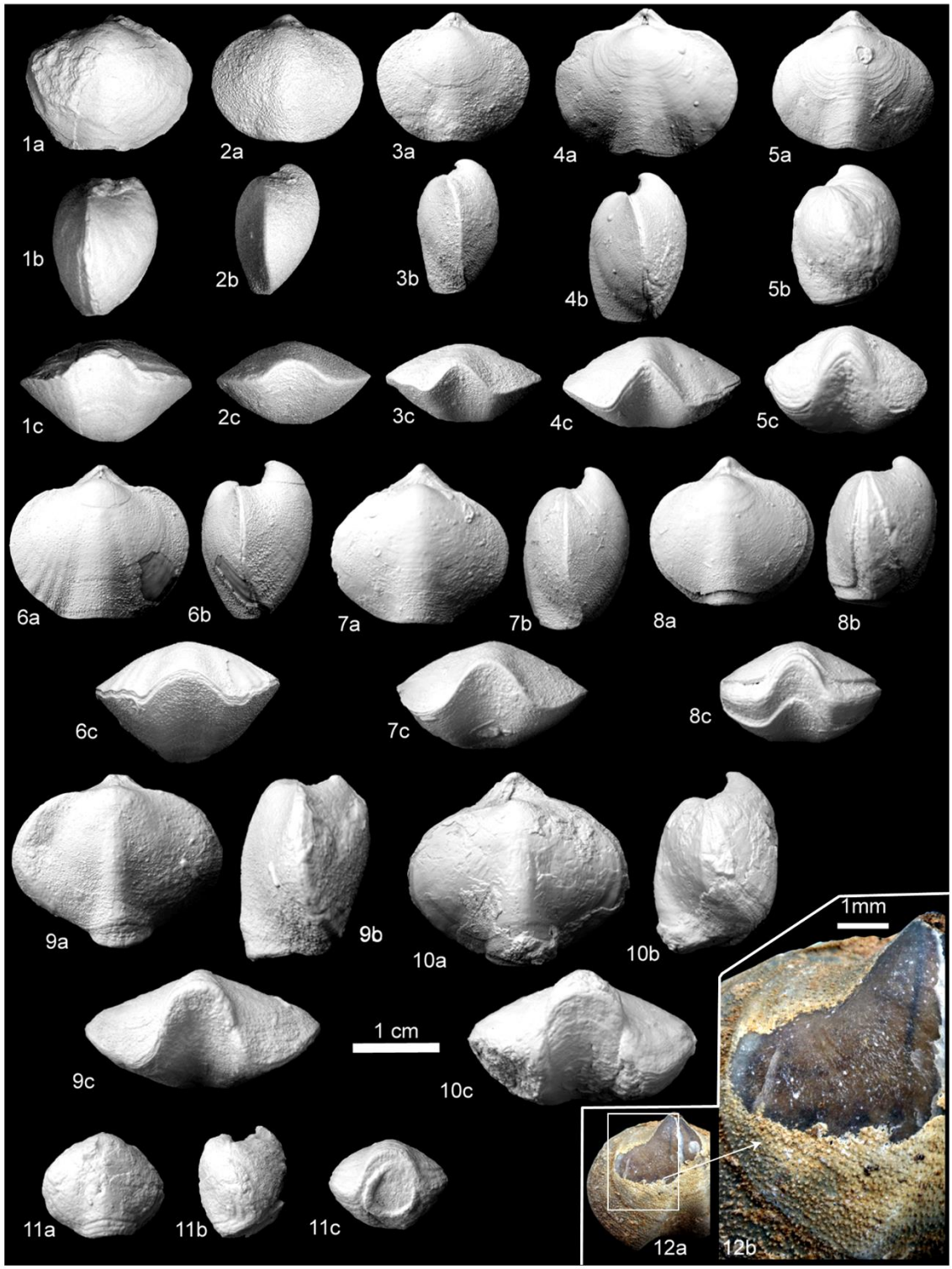


Fig. 9

ACCEPTED MANUSCRIPT

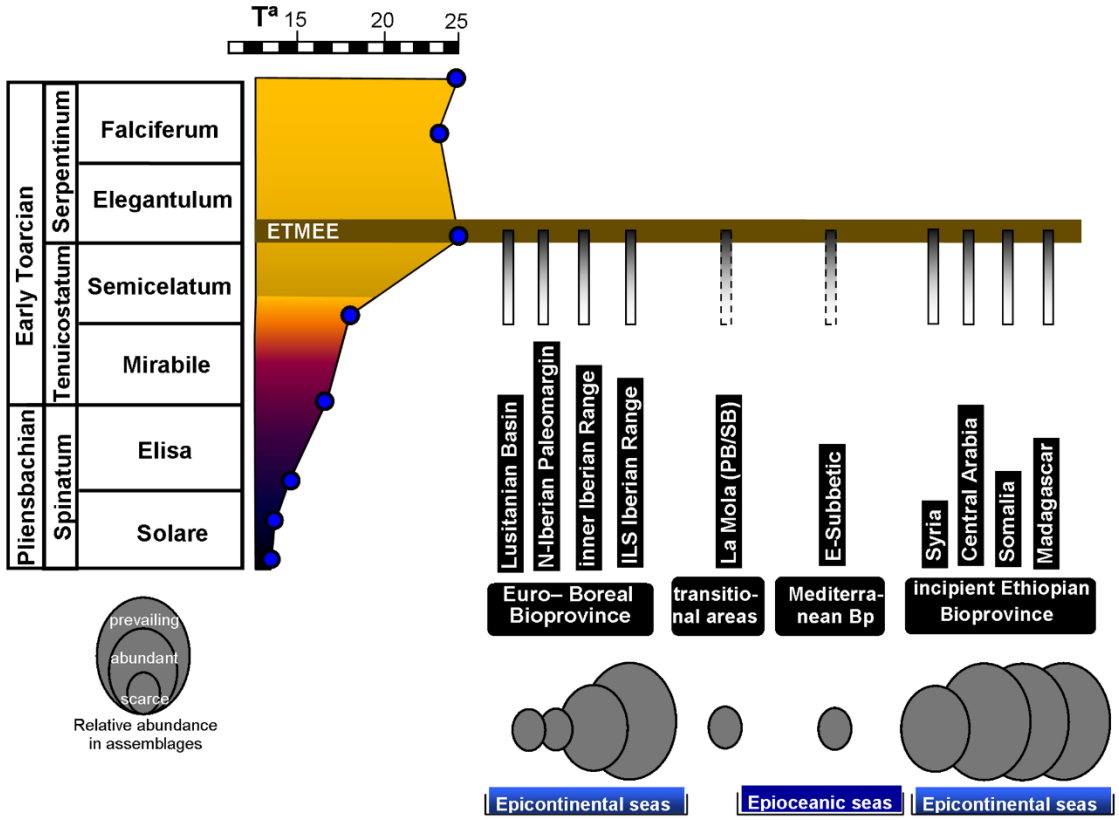


Fig. 10

ACCEPTED MANUSCRIPT

PC	Eigenvalue	% variance
1	109.028	80.918
2	12.4838	9.2653
3	5.56788	4.1324
4	2.6437	1.9621
5	2.30067	1.7075
6	1.29127	0.95836
7	1.05654	0.78414
8	0.366615	0.27209

Table 1: Eigenvalues and relative weight of the axis obtained in the performed PCA.

ACCEPTED MANUSCRIPT

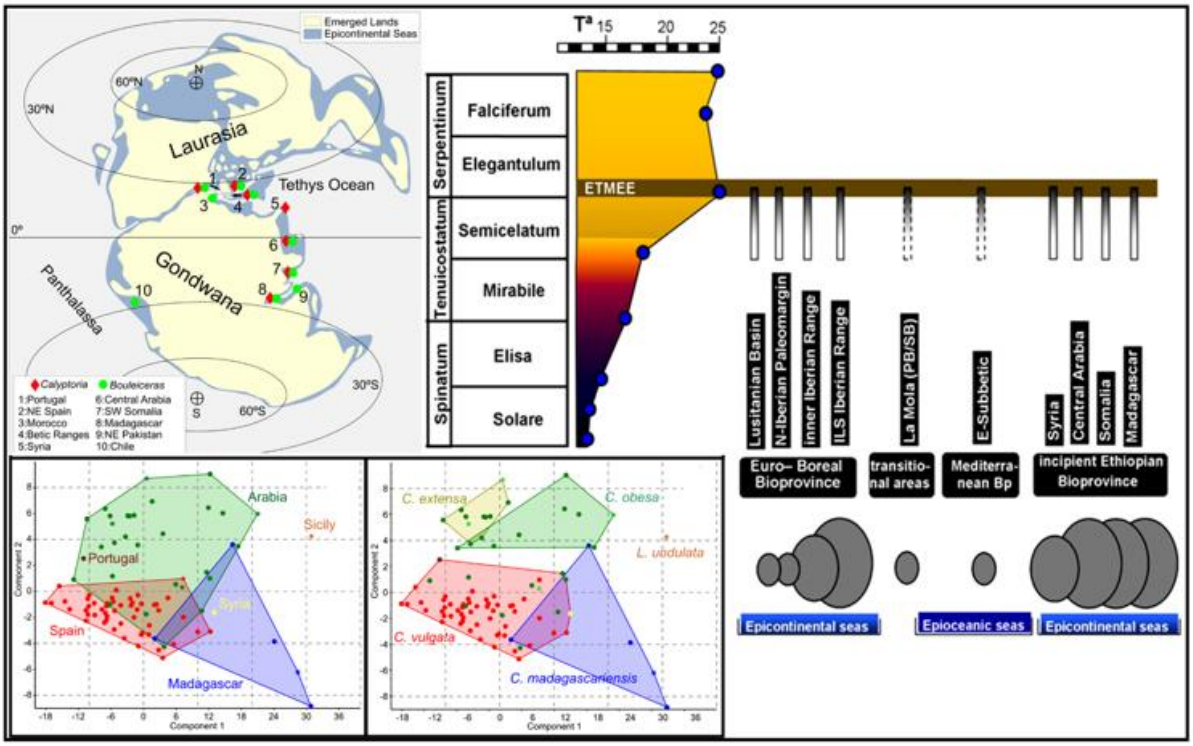
ACCEPTED MANUSCRIPT

Taxa as cited in the original work	Region	Author	Year	Specimens	Proposed attribution (herein)	Remarks
Spiriferina rostrata Schlot. var. *madagascariensis* Thevenin	Madagascar	Thevenin	1908	pl. 5, figs. 2-9	***Calyptoria madagascariensis* (Thevenin, 1908)**	
Spiriferina madagascariensis (Thevenin)	Somalia	Chiocchini et al.	2002	p. 33		(vid.)
Liospiriferina undulata (Seguenza)	Arabia	Alméras	1987	pl. 1, figs. 1-4		
Liospiriferina obesa Cooper	Arabia	Cooper	1989	pl. 19, figs. 36-52	***Calyptoria obesa* (Cooper, 1989)**	
Liospiriferina undulata (Seguenza) morph. *obesa* Cooper	Arabia	Alméras et al.	2010	pl. 1, fig. 10		
Liospiriferina undulata (Seguenza)	Arabia	Alméras	1987	pl. 1, figs. 5-6		
Calyptoria extensa Cooper	Arabia	Cooper	1989	pl. 19, figs. 1-13	***Calyptoria extensa* Cooper, 1989**	
Calyptoria carinata Cooper	Arabia	Cooper	1989	pl. 31: figs. 1-3; pl. 37, figs. 1-21		
Calyptoria statira (Gemmellaro)	Arabia	Alméras et al.	2010	pl. 2, figs. 1-4		
Spiriferina tumida v. Buch var. *haueri* Suess	ILS (Iberian Range)	Bizon et al.	1966	Pl. 27a, fig. 5		
Liospiriferina undulata (Seguenza)	Iberian Range	Rousselle	1977	pl. 1, fig. 10 a-d		
Liospiriferina undulata (Seguenza)	pre-Pyrennes	Calzada	1981	fig. 2, 6		
Liospiriferina vulgata Cooper	Arabia	Cooper	1989	pl. 19, figs. 30-35		
Liospiriferina undulata (Seguenza)	Iberian Range	García Joral & Goy	2000	p. 381, 384		(vid.)
Liospiriferina undulata (Seguenza)	Syria	Alméras &Mouty	2001	pl. 1, fig. 1		
Callospiriferina? *undulata* (Seguenza)	Iberian Range	Comas-Rengifo et al.	2006	fig. 3, 8 a-d		(vid.)
Liospiriferina undulata (Seguenza) morph. *vulgata* Cooper	Arabia	Alméras et al.	2010	pl. 1, figs. 1-5	***Calyptoria vulgata* (Cooper, 1989)**	
(*pars*) *Liospiriferina undulata* (Seguenza) morph. *obesa* Cooper	Arabia	Alméras et al.	2010	pl. 1, figs. 6-9		
Liospiriferina? *undulata* (Seguenza) *sensu* Rousselle	Iberian Range	García Joral et al.	2011	Fig. 4, 5a-c		(vid.)
Liospiriferina? aff. *undulata* (Seguenza)	Portugal	Comas-Rengifo et al.	2013	fig. 2		(vid.)
Liospiriferina? *undulata* (Seguenza)	easternmost Subbetic	Baeza-Carratalá	2013	fig. 6, 7 a-c		(vid.)
Liospiriferina? *undulata* (Seguenza)	ILS (Iberian Range)	Baeza-Carratalá et al.	2016a	fig. 6, 6-7		(vid.)
Liospiriferina undulata (Seguenza)	Betic transitional areas	Baeza-Carratalá et al.	2016b	fig. 4, 12-13		(vid.)

Table 2. Re-arrangement of the representatives of the *Calyptoria* lineage with synonymy of each species herein recognized as valid and attributed to the genus *Calyptoria*. ILS: Ibero-Levantine Sector of the Iberian Range; *(vid.):* specimen directly checked by the authors.

ACCEPTED MANUSCRIPT

Graphical abstract



ACCEPTED

ACCEPTED MANUSCRIPT

Highlights

- Arab-Madagascan faunal dispersal event concurred with warming spike prior to ETMEE
- Brachiopods migrate across North-Gondwana paleomargin to the peri-Iberian platforms
- Inter-tropical controlled spreading depends on the epicontinental seas development
- Reassessment of genus *Calyptoria* supports Iberian representatives in this lineage
- *Calyptoria* was integrated in the stable Iberian fauna pior to extinction in ETMEE

ACCEPTED MANUSCRIPT